VOL. 39, PART 2 JUNE 1956

The British Mycological Society

(Recognosce notum, ignotum inspice)

TRANSACTIONS

Edited by

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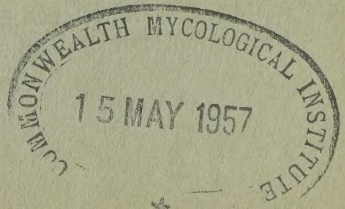
CAMBRIDGE UNIVERSITY PRESS
LONDON: BENTLEY HOUSE, N.W.1
NEW YORK: 32 EAST 57TH STREET, 22



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Enquiries from the U.S.A. should be addressed to the Cambridge University Press American Branch, 32 East 57th Street, New York 22.

Trans. Brit. mycol. Soc. **39** (2), 145–232 (1956).

CONTRIBUTIONS TOWARDS A MONOGRAPH OF THE GENUS *PLUTEUS*

By ROLF SINGER

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(With 66 Text-figures)

The types of most of the species described in *Pluteus* and in other genera, but attributed to *Pluteus*, have been studied. The main classification as adapted from Fayod in modern treatments of the genus is maintained, but some secondary characters such as the shape of the terminal cells of the epicutis, the pigmentation of the pleurocystidia, and the presence or absence of clamp connexions, are introduced as important criteria for the delimitation of species. The best known species of the genus are set out in comprehensive keys (see pp. 222–232).

Since Fayod studied the anatomy of the genus *Pluteus*, numerous contributions to the knowledge of the species of this genus have been made, but not all give the data required by Fayod's classification. New taxonomic characters or emendations of Fayod's criteria have not been proposed, and the main classification remains as outlined by Fayod. The present author treats the species with a non-cellular epicutis in a single Section so that the data are arranged according to alphabetical order of the species within the Sections *Trichoderma* Fayod and *Celluloderma* Fayod. For the subdivision of these Sections the reader is referred to the discussion on classification, p. 220.

In addition to characters of the epicutis and the structure of the apex of the cystidia (which were stressed by Fayod), the author uses some criteria hitherto neglected, such as the presence or absence of clamp connexions, the shape of the metuloids and cheilocystidia, the shape of the spores (whether almost geometrically globose or subglobose to ellipsoid), the presence or absence of a dissolved intracellular pigment in the pleurocystidia, and the shape of the terminal member of the hyphae forming the epicutis of the pileus.

The species of *Pluteus* are very numerous and variable in the tropics and in parts of North America; on the other hand, some European species have had to be neglected because of the absence of type or authentic material. It is felt that the elucidation of the ambiguous species described from Europe can be done only by European workers, who by visiting the type localities and establishing the occurrence of species similar to the published descriptions may obtain topotypes (see the list of species not restudied, p. 220).

The examination of the non-metuloid cystidia is often difficult because they have a marked tendency to collapse in dried material. Mounts in cresyl blue solution have proved to be valuable in such cases. The anatomy

Vol. 39, *Part* 1 *was issued* 20 *March* 1956

of the hymenium and the epicutis should, however, always be studied in ammonia mounts because by the use of dyes any characteristic intracellular pigment is obscured. The spores are easily observed since they are generally plentiful and rather durable, due to the slight thickening of the wall at maturity. Unfortunately, the absolute measurements of the spores are often of little value and should be used with caution and on the merit of each particular case, since many species have spores of widely differing sizes. This does not, however, mean that spore size is never a useful taxonomic character for *Pluteus*.

The representatives of the genus which have been studied included the Spegazzini and Rick types, the Berkeley and Curtis types (mostly from Cuba), the Murrill types from Central America and the United States, the Berkeley and Broome types from Ceylon, the Peck types from North America, some Montagne material preserved in Paris, and the types preserved in the Patouillard Herbarium (Indo-China, tropical America, etc.). Some European species lacking types or type substitutes could only be treated on the basis of traditions established among European writers and where conflicting views prevailed the issue could sometimes be decided in favour of one interpretation.

The author is particularly grateful for access to the types preserved at the Kew Herbarium which were put at his disposal by its Director, Sir Edward Salisbury; furthermore for being able to revise the types preserved at the Paris Museum (Director Dr R. Heim), and at Albany, N.Y. (Peck's types), New York (Murrill's earlier types, kindly lent by Dr D. P. Rogers), Ithaca (Atkinson's types, kindly lent by Dr R. Korf), La Plata (formerly Eva Perón, Spegazzini Herbarium, kindly lent by Ing. J. C. Lindquist), and Porto Alegre (Rick Herbarium, under the custody of Padre B. Rambo). Smaller numbers of species were studied at Gainesville, Herbarium of the Agricultural Experiment Station (by courtesy of Dr Murrill and E. West), Chicago, Palo Alto, Ann Arbor, etc., in addition to earlier type studies at the Farlow Herbarium.

For the citation of these herbaria the recommended abbreviations (*Chron. Bot.* **5**, 143–150, 1939) are used, and for colour names—'R' is cited for Ridgway and 'M. & P.' for Maerz & Paul (1st ed.).

The work leading to the present paper has been done, to a large extent, with a John Simon Guggenheim Memorial Fellowship (1952–3) and with a grant from the American Philosophical Society, Philadelphia (1954) for both of which the author is deeply grateful.

PLUTEUS

1. Section *TRICHODERMA* Fayod (1889)

PLUTEUS AETHALUS (Berk. & Curt.) Sacc. (*Agaricus aethalus* Berk. & Curt.) (Fig. 1)

Spores not geometrically globose but rather short, 4·5–5 × 4·3–4·5 μ; basidia e. g. 22 × 5·5 μ, 4-spored; cystidia now few on the sides of the lamellae, some hyaline, some with fuscous cell sap, vesiculose and often gradually attenuate upward or broadly ampullaceous, e. g. 41 × 15·2 μ;

cheilocystidia similar and also brown inside; epicutis formed of bunches of basically elongate (up to 200 × 13–16 μ) and shorter, more cystidioid (50–120 × 13–20 μ) erect to suberect elements, the majority ventricose in the middle and with attenuate, mostly subacute apex, with equally dissolved or locally condensed brown pigment; similar but often more variable and perhaps more often obtuse elements on the covering of the stipe. Wherever there are very short (ellipsoid or vesiculose) elements in the covering of either pileus or stipe, these are rare, scattered and inconstant. All hyphae without clamp connexions. The carpophores are small, with blackish flocculose edge and densely flocculose-punctate pileus, somewhat more loosely floccose on the stipe.

The type (FH) is, according to data kindly furnished by Dr A. Digilio, identical both at the Farlow and at Kew. This species was also found by R. W. G. Dennis in Trinidad. The type of *A. tephrostictus* seems to be the same thing, but in worse condition.

Agaricus agloetheles Berk. & Br.

This agrees in all characters with *A. curtisii* Berk. (K-type).

Agaricus alborubellus Mont.

The interpretation introduced by Patouillard is incorrect. The type (P) is not a *Pluteus*. The species described by Singer & Digilio under this name, and apparently identical with Patouillard's is a species different from all others known to me and is herewith redescribed as:

Pluteus haywardii* sp.nov. (Fig. 2)

Pileo albo vel pallide umbrinello vel pallide carneolo, subtiliter granulosulo, demum in umbone fibrilluloso-granuloso, margine striato, 12–25 mm. lato. Lamellis pallide salmoneis, latis. Stipite albo, albo-pruinato, 23–27 × 1–1·5 mm. Sporis 5·5–7·2 × 4·8–6·8 μ, globosis vel subglobosis; cystidiis hyalinis, latis, angustatis vel rotundatis ad apicem, 38·5–48·5 × 17·5–21 μ; cuticula pilei ex floccis exiguis trichodermialibus consistente; trichodermio ex elementis elongatis (37–55 × 13·7–29 μ) consistente. Ad truncos et ramos emortuos, Tucumán, T 452, typus (LIL). Cf. *Pluteus alborubellus* (Mont.) Pat., Singer & Digilio, *Lilloa*, **25**, 263, 1951.

Patouillard's specimen, on the basis of which the transfer to *Pluteus* was made, was also studied. This is no. 974 on a branch of *Bignonia pentaphylla* (FH). It looks macroscopically like our own collections. The spores are 5·5–7 × 4·8–6 μ, subglobose (not geometrically globose); elements of epicutis (which has same structure as described above) somewhat longer (terminal elements with broadly rounded tips, with little or no brownish pigment, with some fuscous cell sap in some, e. g. 77 × 19·5 μ).

This is apparently identical with or very close to our own material described above as *P. haywardii* but see also under *P. aquosus*.

Pluteus aporpus Sing. (*Sydowia*, **8**, 122, 1954)

Nothing can be added to the original description.

* Dr Kenneth Hayward, noted entomologist, who has contributed a large amount of interesting fungous material from arid regions.

Pluteus aquosus sp.nov.

A *Pluteo niveo* cystidiis superne latioribus saepe capitatis, substrato lignoso, cellulis terminalibus epicutis pilei ampullaceis, sporis paulum minoribus, stipite apicem versu attenuato, cavo, magis voluminoso differt. Ad truncos Taficillo, Argentinae, Singer T 2208, typus.

Pileus white to watery white, minutely fibrillose on the disc, margin smooth to very short-sulculate, but a sordid pinkish shade appearing in the marginal zone eventually, convex subumbonate, eventually flatter, 20–40 mm. broad. *Lamellae* white, then pink with white to pinkish pallid edge, close to subclose, rather broad, free. *Stipe* white to watery whitish, white sericeous, hollow, tapering upwards but not bulbous, 40–50 × 5–6 mm. *Context* white or watery white, unchanging, inodorous. *Spores* varying from very short ellipsoid to subglobose, but few if any globose, 5·3–6·8 × 4·7–5·7 μ; basidia 4-spored; cystidia hyaline, entire, 48–63 × 10–26 μ, ampullaceous with a very broad 'neck' or with subcapitate apex, rather numerous; cheilocystidia more versiform, sometimes with lobed-crested apex, always broadly ventricose below, hyaline, 40–47 × 9–23·5 μ; epicutis of chains of elongated hyphae, most of them hyaline, some with pale fuscidulous evenly dissolved intracellular pigment, terminal members fusoid-ampullaceous, 80–140 × 9–19 μ, 'neck' obtuse, about 4 μ in diameter; hyphae without clamp connexions.

On rotten Dicot wood in subtropical-montane forest, Argentina, prov. Tucumán, east slope of Taficillo at about 1100 m. alt., 23 February, 1955; Singer T 2208, LIL.

This species keys out with the white species near *P. niveus* and *P. semibulbosus*. It differs from the former in the characters indicated in the key and in the Latin diagnosis, from the latter likewise in shape of cystidia and stipe, etc. *P. haywardii*, which is sometimes as pale as *P. aquosus*, differs in smaller size, different structure of the epicutis of the pileus and different spores, at least in the type collection. Patouillard's collection of what he called *P. alborubellus* (q.v.) is also smaller but seems to be closer to *P. aquosus* as far as some microscopical characters are concerned. It may be a small specimen of *P. aquosus*.

Legends to Figs. 1–6.

Fig. 1. *Pluteus aethalus*. *e*, terminal cell of epicuticular hyphae of pileus, × 500; *s*, spore, × 1000; *c*, pleurocystidium, × 500.

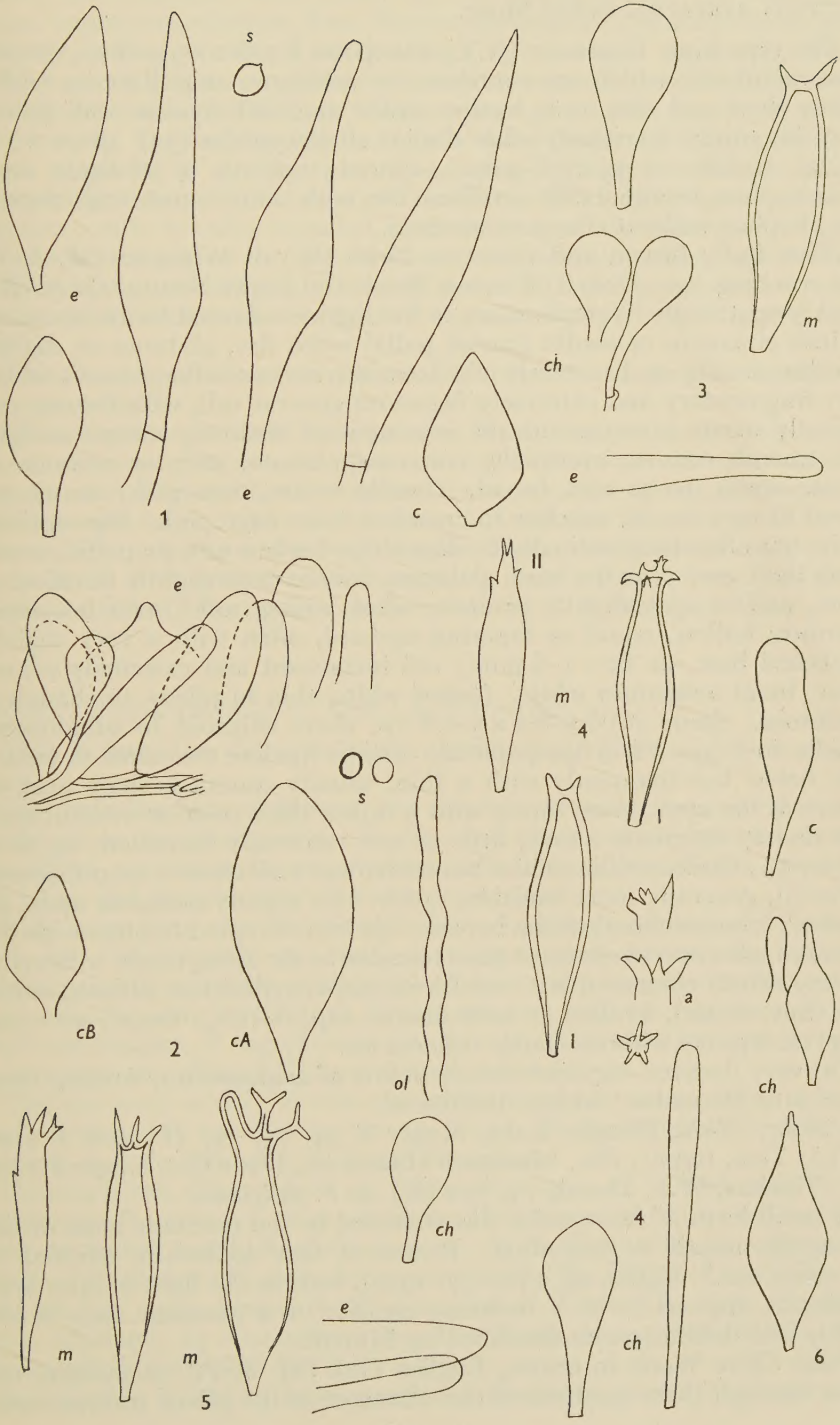
Fig. 2. *Pluteus haywardii*. *e*, elements of the epicutis in their normal position in radial section, × 500; *s*, spores, × 500, *cA*, cystidium, × 1000; *cB*, cystidium × 500; *ol*, oleiferous hypha, × 500.

Fig. 3. *Pluteus atromarginatus*. *ch*, cheilocystidia; *m*, metuloid; *e*, terminal cell of epicuticular hyphae of pileus. All × 500.

Fig. 4. *Pluteus cervinus* var. *brasiliensis* (= *Pluteus xylophilus*). *m*, metuloids, I of form 1 (*Cervinus*-type), II of form 2 (*Magnus*-type); *a*, three drawings of the horned apex, the lowest as seen from above; *ch*, cheilocystidia of two types. All × 500.

Fig. 5. *Pluteus cervinus* var. *minor*. *m*, metuloids; *ch*, cheilocystidium; *e*, terminal cells of epicuticular hyphae of pileus. All × 500.

Fig. 6. *Pluteus citrinus*. *c*, pleurocystidium; *ch*, cheilocystidium. All × 500.



Figs. 1 6.

Pluteus atriavellaneus Murr.

The type from Tennessee (N.Y.) has spores 6·7–8·2 × 5·5–6·7 μ, cystidia (not metuloids) which are ventricose to ventricose-ampullaceous with a rather short and thin neck, hyaline inside and with hyaline wall (which may be thinly incrusted) with similar cheilocystidia (34) 48–70 × 7·8–19·7 μ; basidia 22–33 × 8·2–9·8 μ, 4-spored; epicutis of elongate versiform hyphae, terminal cells versiform but with rather constantly rounded tips; hyphae without clamp connexions.

Pileus Buffy Brown and Chaetura Drab (R.) or Wigwam (M. & P.) but reaching (sec. Dennis) Fuscous Black and Light Neutral Gray (R.), weakly or strongly hygrophanous, in the lighter coloured forms becoming whitish cinereous or sordid greyish pallid when dry, glabrous or slightly fibrillose or silky on disc, rarely with loose tiny sericeous floccons of a white, very fragmentary and extremely fugacious general veil, with short-transparently striate to striate-sulcate or sometimes distinctly sulcate margin, disc smooth convex, eventually convex-applanate, with or without an obtuse umbo, 10–41 mm. broad. *Lamellae* white, then pink, ventricose, broad to very broad, subclose to crowded, free; edge pink. *Stipe* entirely white but often longitudinally hyaline-striped when wet, or pallid, sometimes light grey near the base, glabrous, only at base slightly fibrillose at times, and at apex slightly pruinose when young, solid, soon becoming narrowly hollow, equal or tapering upward, often with a very slightly thickened base, 22–60 × 1–6 mm.; veil inconstant and extremely evanescent; basal tomentum white. *Context* white, thin in pileus, unchanging, inodorous. *Spores* (6) 6·5–8·2 × 5·2–6·7 μ, short ellipsoid to subglobose; basidia 20·5–33 × 7·8–9·8 μ, 4-spored; cystidia hyaline vesiculose to ventricose below but frequently with a thin, usually rounded, short neck or mucro at the apex, more rarely with a rather thick neck or without neck and merely attenuate above, little or not resinously incrusted, 24–82 × 7·8–27·5 μ; cheilocystidia similar but sometimes vesiculose or ampullaceous to fusoid, generally more variable, rarely with slightly nodulose apex, all hyaline; hymenophoral trama inverse; epicutis of repent hyphae with the terminal cell always or in most cases rounded at the apex, rarely with acute mucro, strictly elongated but variable in shape, cylindrical, clavate, subulate (but obtuse), hyaline or with fuscous sap, 8–18·5 μ broad, 30–150 μ long; all hyphae without clamp connexions.

On very decayed logs and woody debris of angiosperms, fruiting from June until December; widely distributed.

U.S.A.: *Mich.*, Douglas Lake, Singer N 54, 75, 327 (F) and T 2101 (LIL); *Tenn.* (type); *Fla.*, Matheson Hammock, Dade Co., Singer F 1409 (F); *Trinidad*, W.I., Dennis 75, 75a (K), as *P. fuliginosus*.

A small form of this species was collected in the montane zone of the Aconquija massif in Argentina. It was at first doubtfully referred to '*P. roberti* var.?' (*Lilloa*, **25**, 256–257, 1952), but, in the light of later type studies, it appears to be a montane nanism or a montane race of the widely distributed species described by Murrill.

Pileus Olive Wood in centre, English Oak (M. & P.) on margin, the latter through three-quarters of the diameter of the pileus transparently

striate, and sulculate when dried, convex, 9 mm. broad. *Lamellae* pink, broad, ventricose, subclose, free. *Stipe* sordid hyaline, glabrous above, subpruinate below, thickened at the base, 15 × 1–2 mm. *Spores* 6·5–7·6 × 4·8–5·8 μ, not globose; cystidia vesiculose to ampullaceous, with a short strongly attenuate apiculus, or with a tapering subulate mucro or 'neck' at the apex, hyaline, 45–55 × 8–12·5 μ, cheilocystidia similar; epicutis of pileus consisting of mostly repent filamentous hyphae, some rather broad towards the terminal end, most of them filled with a gelatinous brownish pigment, with broadly rounded tips; hyphae of the thin-membranous white mycelial pad at the base of the stipe hyaline, bunched together and without clamp connexions. On dead wood of *Podocarpus parlatorei* (coniferous wood) at 1900 m. alt., prov. Tucumán, Taficillo, R. Singer T 1389 (LIL).

This form is now inserted under the herbarium name *P. atriavellaneus* var. *parvus* ined.

The compressed stipe of *P. compressipes* Murr. is undoubtedly a character of no taxonomic importance. The species, if described correctly, would key out with *P. atriavellaneus*, and become a synonym of this species, inasmuch as the latter is widely distributed. I cannot be quite positive on this synonymy because there is a slight chance that *P. compressipes* (q.v.) is the same as *P. spilopus* var. *albostipitatus* Dennis (q.v.); but if not, one might consider it the tropical, larger, form of *P. atriavellaneus* Murr.

Pluteus atromarginatus (Sing.) Kühner (Fig. 3)

This is based on *P. cervinus* var. *atromarginatus* Sing., *Z. Pilzk.* **4**, 40, 1925.

The type has been destroyed, but the data available cannot leave any doubt about the identity of the fungus. It is characterized by the balloon-shaped to vesiculose brown cheilocystidia, horned metuloids, blackish gill edge, and the presence of clamp connexions.

This same form was also described by R. Schulz as var. *nigrofloccosus*. *Verh. bot. Ver. Brandenb.* **54**, 1022, 1912 (1913) and as var. *atromarginatus* Konrad shortly after the publication of my variety which was elevated to the rank of species by Kühner. The name now employed by some European mycologists, *P. nigrofloccosus* (R. Schulz) Pilát is a later synonym of *P. atromarginatus* (Sing.) Kühner if used as species.

The species is widely distributed in the northern hemisphere. I have studied material, in addition to the type, of numerous collections in Europe, and the following in North America:

Canada: *Ont.*, Glen major, 25 September 1932, G. S. Bell, det. H. S. Jackson (as *P. umbrosus*), on sawdust, no. 3873 (Iowa); U.S.A.: *Mich.*, Neebish, on indet. wood, September 1909, S. A. Harper 2544, with good photo, det. Singer (F), also September 1916 (F); Maple River, Emmet Co., 28 July 1953, Singer N 887 on wood of *Tsuga* (F). *Calif.*, Sequoia Park, Oakland, 24 November 1935, Lee Bonar, h.n. 540665 (UC); Lee Bonar 738, h.n. 605652 (UC).

No. 540665 is said to have grown on *Acacia* stump which, if correctly

determined, is the first exception to the rule that this species grows on coniferous wood. No. 605652 has a pileus of 140 mm. diameter, stipe 100 × 17 mm. with slightly swollen base.

Pluteus australis Murr., see under *P. magnus*.

Pluteus avellaneus Murr.

The type has spores 6·5–8·7 × 5·5–7 μ, rarely reaching 9·8 × 7·5 μ; cystidia not metuloid, with brownish cell sap, or entirely hyaline or pale brownish below, with one appendage at apex or often with nodulose apex, or with entire tip which is rounded, with thin, rarely slightly thickened walls, without resinous incrustation or with a very indistinct one, 48–79 × 13–28·5 μ; hyphae with clamp connexions.

The type (NY) comes from Lake Placid, Adirondaks, N.Y. This is one of the few species with non-metuloid cystidia where the hyphae have numerous clamp connexions. *P. umbrinidiscus* Murr. (q.v.) is the same species.

Pluteus brunneidiscus Murr.

The type (NY) from Connecticut was collected by Earle (524), and belongs in the *Cervinus* group. The metuloids have 2–4, mostly 3 acute or more rarely obtuse strong apical prongs; the epicutis of the pileus is composed of extremely elongate, but very voluminous hyphae; all hyphae with clamp connexions. This reminds one of *P. salicinus*, but the colour is different and the centre of the pileus does not show any erect spinules; the base of the stipe was neither green nor blue. This is therefore an independent species close to *P. salicinus*, and very close to *P. washingtoniensis* Murr. and *P. subcervinus* (Berk. & Br.) Sacc.

Pileus umber, greyish brown, sordid fawn coloured, glabrous, only on the disk often with innate fibrillose squamules, smooth, convex or conical-applanate with declivous margin eventually irregularly convex-applanate or subplane, 33–48 mm. broad. *Lamellae* white, then beautifully pure rose colour, broad, ventricose, close, free. *Stipe* entirely white, flocculose pruinose at apex but usually glabrescent, glabrous below, smooth and somewhat shining, subequal or equal or tapering upward, becoming hollow 32–57 × 3–8 mm. *Context* white, unchanging, even in the base, inodorous. *Spores* 7–8·5 × 4·8–6·2 μ; basidia 27–31·3 × 7·8–8·3 μ, 4-spored; metuloids 50–67 × 15·3–18·2 μ, moderately thick walled, often moderately numerous, hyaline, with (2)–3 or (2–3)–4 rather high subacute to acute, or sometimes rounded (but then provided with minute secondary apical warts) apical prongs, ventricose in the middle; cheilocystidia clavate 45–70 × 10–20 μ, often intermixed with prongless metuloids, all hyaline; epicutis of pileus consisting of elongate hyphae, which are voluminous, cylindrical or fusoid or long-ventricose to clavate, with the apex often attenuated but always rounded, 78–200 × 8·5–27·3 μ; hyphae with clamp connexions (but sometimes some septa without a clamp observed).

On rotten stumps, July-September.

U.S.A.: *N.Y.*, Adirondaks, Huntington Forest, Singer 27 (FH); Atkinson, Lake Piseco, h.n. 14460 (CU); *Conn.*, type (NY).

The Atkinson collection differs slightly from the two others by having a larger number of metuloid prongs with rounded tips and secondary appendages, and more broadly ampullaceous than clavate cheilocystidia (those of the type not observed), but I believe that this collection still belongs in the same species.

Pluteus cervinus (Kummer ex Fr.) Sacc. (*Agaricus cervinus* Schaeff. ex Fr.)

The species commonly found and corresponding to the original description lacks clamp connexions. A type specimen does not exist, but the species considered as typical has well-developed horns or prongs on the metuloids, and spores reaching 8μ and more. There are no metuloids of a second type (acute and non-pronged), and the cheilocystidia are all of one type: vesiculose-clavate to balloon-shaped. The epicuticular hyphae are strongly elongate. The stipe is mostly innately fibrillose (or sometimes somewhat scabrous) from elongate hyphae with fuscous cell sap.

This is the type species not only of the section *Trichoderma* Fay., but of the genus *Pluteus*. It is very variable as far as spore size and cystidia and cheilocystidia are concerned, and there is no absolutely sharp line of demarcation between this and what we call *P. curtisii*, even though the two extreme types are easy to distinguish. In *P. curtisii*, there is a definite dimorphism in the metuloids; the spores are usually somewhat smaller, and the pileus is lighter coloured with more brownish scales in the centre; the stipe usually lacks the fuscous fibrillosity of the type form. Moreover, both types of metuloids have a tendency, in *P. curtisii*, to form lateral spines and prongs in addition to, or instead of, the apical ones. To begin with the last character, it has been shown by several observations that the tendency to form lateral spines and prongs increases with the age of the carpophore, so that it is quite common to find only apical prongs in young carpophores of *P. curtisii*. The dimorphism of the metuloids is also not a very sharp character, in so far as in otherwise quite typical *P. cervinus* one may occasionally observe a very small number (perhaps one or two per preparation) of acute, not horned metuloids among the cheilocystidia. The size of the spores is likewise not fully constant and spores above 8μ can be found in occasional spore prints from otherwise typical *P. curtisii*. The colour of pileus and stipe seems to be rather constant, yet, there is a complication because of the existence of two forms, both combining the microscopical characters of *P. curtisii* with the general aspect of *P. cervinus*:

(1) A boreal form with spores (6) 6·5–9 × 4·5–5·2μ, otherwise microscopically like *P. curtisii*, macroscopically like *P. cervinus*. This form is without a name as far as I am aware.

(2) A neotropical and South-American montane form with spores 5·5–7 × 3·8–5·8μ, thus as in *P. curtisii*, and with all other microscopical characters as in the latter except for the dimorphism of the cheilocystidia which are partly of the shape typical for *P. cervinus* and *curtisii*, partly elongate as in *P. magnus*. Macroscopically as *P. cervinus*. This has been described as *P. cervinus* var. *brasiliensis* Bres.

(3) A small-spored form, otherwise like *P. cervinus* (see under *P. lilacinus* Mont.).

Pluteus cervinus var. *brasiliensis* Bres. (Fig. 4, 44)

The type has not been studied and probably does not exist. However, the spore character, combined with what we know about species of the *Cervinus* group occurring in South America leaves no doubt about the determination of Bresadola's variety. We have, indeed, a specimen collected likewise in South Brazil which corresponds macroscopically perfectly with material collected by Singer in Argentina, and microscopically, it shows the following characters:

Spores 5·6–6·5 × 4–4·7 μ; basidia 4-spored; *cheilocystidia* dimorphic, (1) long-cylindrical-clavate, 53–73 × 8–12 μ, (2) short-vesiculose e. g. 14·5 × 12 μ, with transitions between the two extremes (of which form (1) is the more common) whereby there is a globose to clavate head-portion with long pedicel (44–54 × 12–15 μ); *metuloids* trimorphic, (1) the majority of those away from the edge with very thick wall (in fully mature specimens) and conspicuous acute to obtuse horizontal, oblique or erect horns, wall reaching 2·7 μ in diameter in the apical region, and thin in the lower 25 μ, ventricose, and the outline above the thickest point forming a straight line toward the pronged apex, more rarely ventricose-subampullaceous as in many Inocybes, 65–77·5 × 12–20 μ, prongs all apical, or in a small minority 1–2 prongs lateral; (2) in the region near the edge of the lamellae of the form often seen in *P. harrisii*, i.e. with tiny horns 2–2·7 μ long or with merely 1–3 granular excrescences of about 1 μ diameter, or else, rarely, with subacute prongs but recurved horizontally, never erect, with thick wall in upper portion, 40–43 × 16–20 μ; (3) a fusoid to subulate form with 1–4 subapical or apical small horns, or without them, varying from more or less thick-walled to thin-walled (the latter a transition to the cheilocystidia); the obtuse forms of metuloid (1 and 2) common and numerous, but form 2 sometimes very rare in other, especially younger, Argentine material, form 3 always present, but always very scattered to rare (often only 1–2 per preparation); epicutis as in *P. cervinus*; hyphae without clamp connexions.

See also *Entoloma xylophilum* Speg.

Pluteus cervinus var. *tucumanensis* Sing. in Sing. & Digilio

A revision of the type (LIL) shows the description as given in the original account (*Lilloa*, **25**, 254, 1951) as essentially correct, but the edge is in poor condition, although it still shows a number of vesiculose cheilocystidia of the *Cervinus* type, and only one elongate cheilocystidium was seen, but it is possible that a majority of the elongate ones have collapsed and are now individually unrecognizable. The metuloids are strongly horned with obtuse or subacute prongs, projecting considerably, and occasional metuloids have lateral prongs in addition to the apical ones. Unless material with exclusively short-vesiculose cheilocystidia is found in the montane zone of Tucumán, it must be assumed that the type is identical with the para-type which has the same dimorphic cheilocystidia as var. *brasiliensis* but metuloids of only one kind: relatively thin walled with long conspicuous horns which have a lumen because of the thin wall and are often bifid to trifid. This is a young specimen, and is certainly conspecific with var.

brasiliensis from which it differs mainly in smaller size and monomorphic metuloids.

While both var. *brasiliensis* and var. *tucumanensis* have a tendency to occur solitary or in small groups, we have also a luxuriant type growing densely gregarious on what seems to be accumulated litter or sawdust in Tingo Maria, Perú, determined by Singer as var. *brasiliensis*, and certainly belonging to this variety (or better, species) as a habitat form. The metuloids are trimorphic, with form 1 very common (prongs often bifid or trifid), form 2 very rare, and form 3 scattered although more numerous than in var. *brasiliensis*; cheilocystidia distinctly dimorphic as above. The pileus reaches up to 90 mm. diameter; stipe 100 × 5–7 mm., thicker below in some.

See also *Entoloma xylophilus* Speg. and *Agaricus lilacinus* Mont.

Pluteus cervinus var. *minor* Sing. (Fig. 5)

The type from the Valley of the Rivera de Sant Maurici near Espot, Spain, Catalonian Pyrenees (BA) is in good condition. It was first studied in 1934 and 1936, then re-examined in 1953. The spores are 6·5–7·5 (8·5) × 5–6 μ, short-ellipsoid, stramineous, smooth; basidia 23–27 × 8·3–10 μ, 4-spored; cheilocystidia clavate-vesiculose, of the *Cervinus* type, i.e. all broad, strongly elongated cells absent; metuloids mostly of the *Cervinus* type, i.e. not attenuated in a straight line formed by each side wall in optical section in the upper portion and always with more than one, actually with (2)–3 acute, more rarely obtuse, simple or forked horns which are well developed and about 7·5 μ long; wall of the metuloids thick, 2·3–3·5 μ in diameter, hyaline; general measurements of metuloids 60–90 × 11–20 μ, most frequently 68–78 × 13·5–16 μ; the only exception to the rule of *Cervinus*-type metuloids is a very rare occurrence of metuloids with small lateral spines (1–2), but in entire sections these may be absent. Hyphae of the epicutis of the pileus strongly elongate, few relatively broad and short, all broadly rounded at the apex, some with slightly thickened wall; all hyphae without clamp connexions. This form was collected on coniferous wood. It differs from typical *P. cervinus*, not only by the smaller spores but by the smaller size of the entire carpophore. The pileus is about 30 mm. broad; the stipe is thin and fragile, relatively slender, and white.

This variety may be considered as a species unless transitional forms can be found in Europe: there is so far no report of these. *P. cervinus* var. *minor* is closest to a form observed in the montane Alnetum of South America, a form which has been described as *P. cervinus* var. *tucumanensis* (q.v.), but I suspect that this is actually a smaller form of *P. xylophilus* (Speg.) Sing. (q.v.).

Pluteus cervinus var. *nigrofloccosus* R. Schulz, and var. *atromarginatus* Sing., see *P. atromarginatus* (Sing.) Kühn.

Pluteus cinereus Quél.

The type has never been revised, and may not exist. The current interpretation is that of Lange, *Fl. Agar. Dan.* **2**, 85, p. 71, fig. D, 1936, which is likely to be correct.

A very similar but slightly smaller form with deeper coloured pileus, paler-coloured stipe, long-sulcate (on drying, splitting) margin and with pleurocystidia (the European form is reported to have no pleurocystidia, fide Kühner & Romagnesi), also with slightly different cheilocystidia, was found in Florida. Because of its very pale stipe, one may confuse it with *P. cubensis* or *P. floridanus*, but its spores are intermediate between the spores of these two species, and neither one of them has the characteristic network of veins. I call it **Pluteus cinerellus** sp.nov.

Pileo centro venoso-reticulato venis pallidis projicientibus, margine per medium radii sulcato, in siccis sulcato-subfisso, atrobrunneo at margine atrobrunneo-granulari vel brunneo-granulari, granulis demum sparsis coloreque tunc pallidiore, centro subobscuriore ('mummy brown' R. vel subobscurius colorato) sed venis subpallidis diluto. convexo umbonato, 12–25 mm. lato. *Lamellis* sordide roseolis, ventricosis, moderate confertis, liberis. *Stipite* albo-griseo, pallide flocculoso-pruinato de apice ad basin, acquali vel plerumque leniter subbulboso, 18–25 × 1·5–2 mm. Carne alba, inodora. *Sporis* 5·7–7·5 × 5–7 μ, rare globosis, plerumque subglobosis, frequenter ovoideis vel breviter ellipsoideis; basidiis 7·8–8 μ latis, tetrasporis; *cystidiis* cc. 40 × 14·5 μ vel minoribus, vesiculosis vel vesiculoso-ampullaceis, hyalinis; cheilocystidiis cc. 40 × 11·5 μ, ampullaceis, apice 4 μ diametro, hyalinis; epicute pilei e strato palisadico depresso consistente, hyphis ventricosis vel cylindraceis, hyalinis vel fuscidulis (e pigmento disoluto intracellulari), apicibus rotundatis, longitudine quinquies latitudinem aequante, 43–86 × 7·8–15 μ; hyphis defibulatis. Ad truncum vetustum delapsum (Caryae?) in dumeto humido ("low hammock") 28 August 1942, Singer F 427, Highlands Hammock State Park, Florida (F).

Pluteus citrinus Murr. (Fig. 6)

The type (FLAS) from Magnesia Springs, Fla., on oak log, has spores 6–6·8 × 5–5·8 μ; basidia 38 × 8·5 μ, 4-spored; cystidia non-metuloid, clavate e. g. 66 × 16·6–20 μ, rather scattered; cheilocystidia ventricose below the middle or in the middle, narrowed to an acute or subacute tip, or subcapitate above, numerous, 42–110 × 11·3–28 μ; epicutis of elongated hyphae with broadly rounded tips, with hyaline or light brownish sap; hyphae without clamp connexions.

Pluteus compressipes Murr.

The type (NY) from Castleton Garden, Jamaica, W.I., is accompanied by a crude painting which shows the fungus somewhat larger than would be expected from the specimen, with striate margin, fuscous avellaneous pileus and white stipe, on wood. Spores 6–7 × 5·5–6·5 μ; basidia and cystidia not preserved but definitely no pronged metuloids present; epicutis of repent, elongate hyphae with rounded tips: clamp connexions none. See also *P. spilopus* var. *albostipitatus* Dennis, and *P. atriavellaneus* Murr.

Pluteus conizatus (Berk. & Br.) Sacc. (*Agaricus conizatus* Berk. & Br.) (Fig. 7)

There are good specimens at Kew, and a good drawing at the British Museum (Broome Herbarium). There is no doubt that both refer to the type, from Ceylon, no. 757. Spores 5·3–7·2 × 4·5–5·5 μ. I take the following anatomical data from the largest specimen (K), which corresponds best with the painting in order to co-ordinate the macro- and microscopical

characters. In other carpophores (which are smaller) one can encounter another type of cystidium with thin walls and brown cell sap, and there the wall is surrounded by a pseudo-membrana which is actually a continuous resinous incrustation and hyaline to pale stramineous (in specimen mounted at the left, and showing no umbo in cross-section). The largest carpophore with umbo which I consider as holotype, was 72 mm. broad and grey on the umbo, with avellaneous striate margin, and finely rivulose surface; stipe yellowish, 105 × 6 mm.; context white (in fresh condition); cystidia metuloid with thin (0·3 μ) to thick (0·7–1·6 μ) walls in upper half or third, but without any prongs, ventricose in the middle, ampullaceous and pedicellate, sometimes subfusoid, with rounded apex, with hyaline to fuscidulous contents, e. g. 70 × 13–19 μ; epicutis a palisade, but rather fragmentary because of the rivulosity of the cuticle, the palisade consisting of 5·5–6 μ broad hyphae with broadly rounded tips, often septate and with internal fuscous pigment bodies; hyphae without clamp connexions.

The frequently thick-walled cystidia and the yellowish stipe distinguish this species. It is possible that some of the specimens preserved with what I designate as the holotype, are either younger carpophores of the same, or another species mixed in (collecting period of the type assemblage indicated as 'October–November'), p.p. possibly *P. glyphidatus*. The latter differs in having cystidia with hyaline contents and of different shape.

Pluteus cubensis (Murr.) Dennis (*Nolanea cubensis* Murr.)

The type from Santiago de las Vegas, Cuba (NY), no. 155, on a piece of thin board in a coffee plantation has short ellipsoid spores, 6·5–8·8 × 5·5–7·3 μ; cystidia without fuscous cell sap, ventricose or cylindric-clavate, thin-walled, without prongs, but sometimes with irregular nodules at apex; epicutis of pileus hyphous, forming radial filaments consisting of elongated elements, the terminal member moderately voluminous and broadly rounded at tip; hyphae without clamp connexions.

This species is rather widely distributed and not uncommon in Central and South America. It was also found in Trinidad by Dennis (no. 15a), on bamboo debris. The aspect of the pileus is that of a deep coloured *Inocybe* with radially fibrous and often rimose cuticle. The surface of the stipe of the type as well as of the other collections has either microscopical fuscous fibrils or macroscopically visible small floccons near the base which consist of elongate hyphae with fuscous cell sap. Before it was known that Murrill's *Nolanea* is actually a *Pluteus*, we could not determine this species correctly, and described the Argentine material as *Pluteus* spec. (*Lilloa*, **25**, 260, 1951; Singer T 352, LIL).

Pluteus cubensis is a very variable and therefore deceptive species. For that reason we add a new description based on all our material:

Pileus Biskra (pl. 16 A 12, M. & P.) in the centre and Brown Sugar (pl. 15 H 10 M. & P.) on the margin, also Bister (R., fide Dennis), often with nearly white margin since the colouring is due to fine silky fibrils which are dense on the disc and become frequently very scattered toward the margin, the fibrils at first when quite fresh somewhat squarrulose, but on drying applicate, and forming granular or finely fibrillose punctations,

towards the margin splitting in an *Inocybe* fashion along the depressions of the sulcate margin and therefore appearing rimose with the white flesh showing through when well-pigmented, merely sulcate in the manner of *Russula puiggarii* when not well-pigmented, slightly hygrophanous if the fibrils are not dense, and especially when old, 17–38 mm. broad, campanulate to convex, often convex with steeper marginal region, eventually applanate, but mostly slightly umbonate.

Lamellae white, then pink, edge always concolorous with sides, subclose to close, moderately to rather broad, somewhat ventricose in many caps, free.

Stipe white, often seen longitudinally striate in mature specimens, very finely (lens) fibrillose, more distinctly fibrillose and somewhat concolorous with the centre of the pileus at the base, solid, subequal with slightly thickened base, or slightly tapering upwards, the brown-fuliginous fibrils of base so indistinct that they can be distinguished only with a lens, always microscopically, with pure white mycelial felt at base, 15–40 × 2·5–3 mm. *Context* white, inodorous. *Spores* 6·2–8·8 × (5) 4·5–7·3 μ, subglobose; basidia 22·3–24·3 × 7·2–9 μ, clavate, 4-spored; cystidia elongate-ventricose or ampullaceous, often somewhat granular-incrusted at apex, hyaline, thin-walled, with entire apex, rarely with nodulose excrescences; (30) 41–73 × (11) 13–20 (33) μ; cheilocystidia similar but more variable, especially tending to be vesiculose, all hyaline, numerous; epicutis of pileus with elongate elements which are completely and evenly filled with the brown dissolved pigment, the terminal ones often cylindrical, clavate, or ampullaceous, always with broadly rounded tip; in the poorly pigmented forms similar elements are also encountered without pigment; dermatocystidia of the stipe versiform (shape of cheilocystidia), hyaline, at base of stipe with brown sap; all hyphae without clamp connexions. On thin boards, on bamboo, on very rotten frondose wood, and on humus, fruiting during the rainy seasons. West Indies south to Argentina.

In some of the darker forms, the rimosity of the pileus is hardly visible and the cystidia tend to be relatively shorter and less ampullaceous, and the spores slightly smaller than average. This combination of characters (as in Argentine material, T 2123, LIL) has nothing to do with the age of the carpophores. The fibrils are in this case more pustulose-squarrulose, although very small. In this collection, the centre of the pileus is Owl, margin Santos (M. & P.). I am not certain whether this is an extreme form of *P. cubensis*, or a closely related, autonomous form.

Legends to Figs. 7–12.

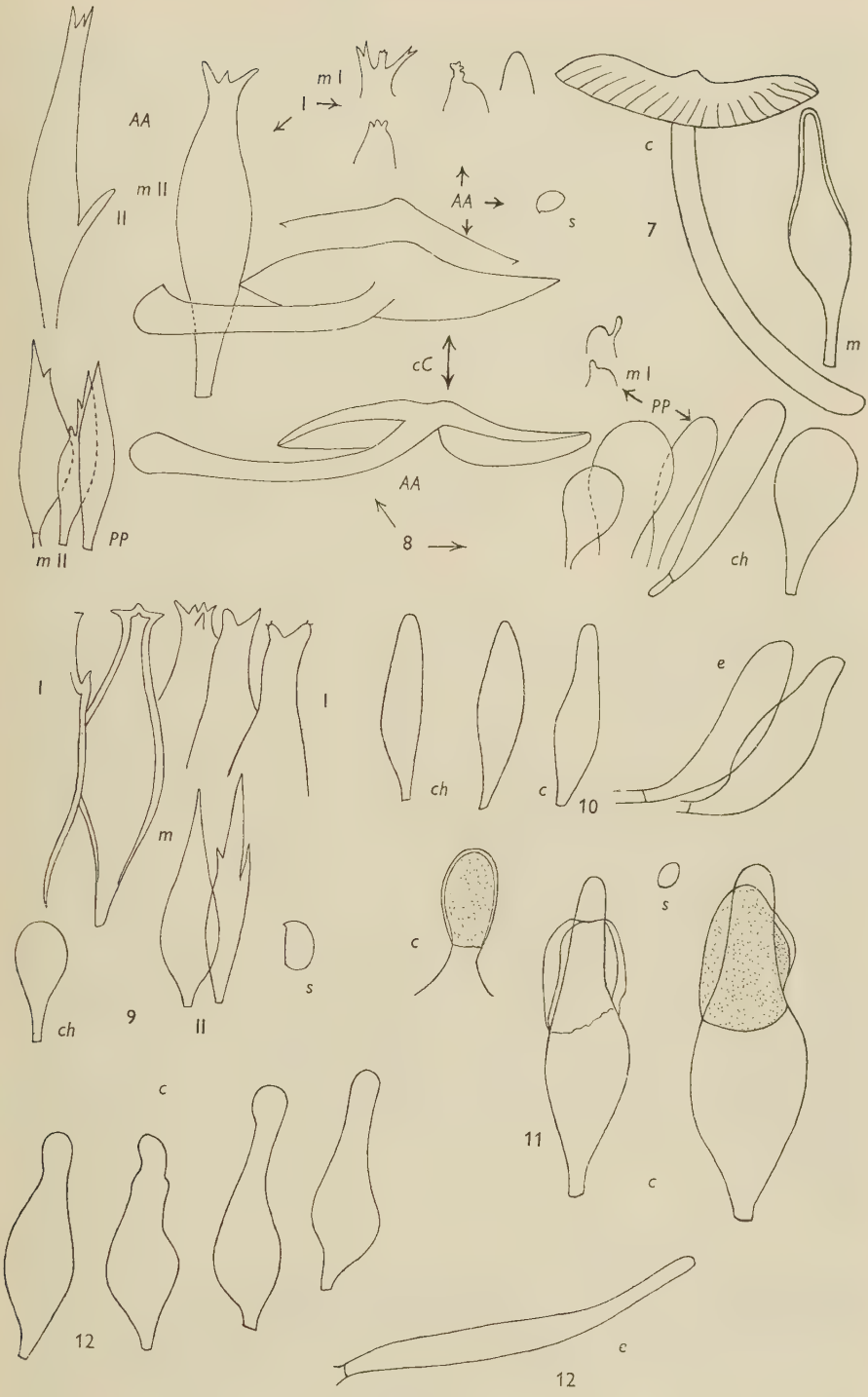
Figs. 7, 8. *Pluteus conizatus*. *m*, pleurocystidium, × 500; *c*, carpophore, half natural size. *Pluteus curtisii*, European and Asiatic material, *m* I, metuloids of form 1 (*Cervinus*-type), *m* II, of form 2 (*Magnus*-type); *s*, spore; *cC*, carpophores, from fresh material (painting in British Museum), half natural size; *ch*, cheilocystidia. All details × 500. Drawings made from the type of *Agaricus agloeotheles* are marked *AA*; those from British collections, determined as *Pluteus patricius*, are marked *PP*.

Fig. 9. *Pluteus curtisii*. American material, *m*, metuloids; I, of form 1 (*Cervinus*-type); II, of form 2 (*Magnus*-type), × 500; *ch*, cheilocystidium, × 500; *s*, spore, × 1000.

Fig. 10. *Pluteus depauperatus*. *ch*, cheilocystidia; *c*, pleurocystidium; *e*, elements of the epicutis of pileus. All × 500.

Fig. 11. *Pluteus diptychocystis*. *c*, pleurocystidia; *s*, spore. All × 500.

Fig. 12. *Pluteus fastigiatus*. *c*, cystidia; *e*, element of the epicutis of the pileus. All × 500.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Figs. 7–12.

Pluteus curtisii (Berk.) Sacc. (*Agaricus curtisii* Berk.) (Figs. 8, 9)

The type (K, FH) from South Carolina was accompanied by coloured pictures (now in Cooke's collection, K) which show white pileus and stipe, and cinnamon-ochraceous squamulose centre, broad lamellae and the general habit of the fungus best known in Europe as *P. cervinus* var. *patricius*. There is also material in the British Museum. The spores are 5·8–8 × 4·5–6·5 μ; basidia 4-spored; cheilocystidia vesiculose as in *P. cervinus*, e. g. 43·5 × 20 μ; metuloids distinctly dimorphic, form 1 of the ordinary *Cervinus* type, with thick to very thick walls in the upper two-thirds, with acute prominent apical prongs e. g. 74·5 × 21 μ, fusoid and often fusoid-ampullaceous much as in many Inocybes; form 2 always abundantly to fairly well represented near the edges of the lamellae, ventricose at or below the middle, often acute and bifid, or with 1–2 lateral spinules below the apex, less thickly walled than form 1, 50–73 × 10–21 μ; hyphae of the white portion of cuticle of pileus consisting of strongly elongate hyphae, arranged radially, repent or slightly ascendant, terminal cells often brownish now, attenuated toward a broadly rounded tip or cylindrical, e. g. 61 × 14·3 μ; more pigmented hyphae on the disc; no clamp connexions.

The three original collections at Harvard are perhaps mixed with *P. cervinus*, but the collections at Kew do not leave any doubt. No. 1523 seems to be the holotype, but at Harvard, as the Kew specimen shows, it is, evidently incorrectly, accompanied by a rather misleading description which mentions a liver brown pileus, but this was apparently taken by Berkeley as corresponding to the older stage. The young stage, as Berkeley saw it, must be represented by specimen 'No. 1, Aug. 1849' which is preserved on the same sheet at Kew. In reality, the liver brown specimens are probably carpophores that have suffered from poor preparation, or else this note reflects a muddle by the collector of *P. curtisii* and *P. cervinus*. The holotype at Kew is unquestionably the species as described above, and furthermore the same as *P. agloeotheles* and *P. patricius*.

I have abundant material of this species: U.S.S.R., Karelia, Kivatch Freindling & Singer, September, 1936, on *Betula*, LE.; England, Surrey, E. Gray comm., det. E. M. Wakefield (as *P. patricius*), on sawdust on edge of wood, 19 August 1945, K.; Ashridge by Monument, D. A. Reid, on *Fagus*, K; U.S.A.: S. C. (type); Fla., Alachua Co., Planera Hammock, Singer F 1667c, 22 January 1943, on *Quercus laurifolia*, F; also F 1667b, F; Dade Co., Matheson Hammock, Singer F 968, on and around old frondose trunk, F; Mich., Cheboygan Co., Singer N 386, 3 July 1953, on coniferous stump, F; also N 467, F; Ceylon, Peradeniya (type of *P. agloeotheles*, q.v.).

Pluteus defibulatus Sing.

The type (LIL, MICH) is, in spite of some discrepancies in the descriptions, apparently identical with *Mycena jaffueli* Speg. (q.v.).

Pluteus depauperatus Romagnesi (Fig. 10)

Thanks to the courtesy of Dr Romagnesi, I have an authentic specimen from the Forêt de Fontainebleau, collected by various delegates of the VIII International Botanical Congress, and determined by Romagnesi (LIL). The spores are $6–8 \times 5{\cdot}3–6{\cdot}2\,\mu$, short ellipsoid or subglobose; the cystidia hyaline, ampullaceous-pedicellate, smooth, thin-walled, moderately numerous, e. g. $50 \times 11\,\mu$; cheilocystidia numerous, hyaline, ventricose-fusoid, or vesiculose-subelongate, $40–50 \times 10–12\,\mu$. Epicutis consisting of interrupted fragments of a trichodermial palisade, i.e. bunches of hyaline to pale fuscous cystidioid hyphae, the terminal cells varying from clavate to ventricose-fusoid, $46–54 \times 9–20\,\mu$; all hyphae without clamp connexions; pigment dissolved, intracellular. This species has probably been called *P. roberti* by some European mycologists.

Pluteus diptychocystis Sing. (Fig. 11)

The type is different from all other types studied (LIL, MICH). I can add nothing to the data published in the original diagnosis (*Sydowia*, **8**, 123, 1954).

Pluteus escharites Berk. & Br.

The original picture in the Broome collection (B.M.) refers probably to a *Rhodophyllus*. There are three specimens at Kew, one of which is a *Pluteus* with spores $5{\cdot}3–5{\cdot}5 \times 4{\cdot}8–5{\cdot}3\,\mu$, only $0{\cdot}1–0{\cdot}3\,\mu$ longer than broad, globose; epicutis consisting of strands or erect fusoid parallel hyphae ($158–190 \times 11–15\,\mu$), all subacute, rarely rounded-obtuse at the tips, umber brown from an intracellular dissolved pigment inside, and rising from a hypodermial layer with the aspect of a subhymenium, consisting of very small, slightly elongated elements; this palisade interrupted and replaced by similar but shorter elements which are more frequently rounded above (hence the 'squamulae minutissimae'); hyphae without clamp connexions.

Since the picture and the upper unnumbered trio of specimens refer to a *Rhodophyllus*, and only one specimen (868, December 1868, from Peradeniya) refers to a *Pluteus*, there is a question whether or not this is a good species from the nomenclatorial point of view. The description does not necessarily exclude the *Pluteus* but it is slightly influenced by the drawing. On the other hand, the numbered specimen is apparently an independent species of *Pluteus*, in spite of the fact that it was impossible to decide whether or not there are pigmented cystidia since the latter had all collapsed in the herbarium specimen. There are brown vesiculose bodies in the hymenium, with spores sticking to them, but they do not revive. Nevertheless, it seems best to designate the numbered specimen below as the holotype, rather than to propose the binomial as *nomen confusum*.

Pluteus fastigiatus Sing. in Sing. & Digilio (Fig. 12)

The type (LIL, MICH), Singer T 1054, is very close to, but hardly identical with, *Pluteus spilopus* (Berk. & Br.) Sacc. (q.v.). Additional material (Singer T 2129, LIL) grew on humus. The spores of four-spored material

are 6·6–7·3 × 5–6·5μ. The cystidia are ampullaceous and quite hyaline, smooth, entire, moderately numerous on both sides and edges of lamellae, 51–80 × 13·2–30μ; cheilocystidia similar or often more short-ventricose to vesiculose-clavate, e. g. 21·5 × 11·3μ, the pleurocystidia sometimes with slightly subcapitate apex, sometimes with a moderately thickened wall (0·8μ) but usually thin-walled; epicuticular hyphae all broadly rounded at the apex, with evenly dissolved fuscous pigment, some broadest (15μ and broader) in the cell underneath the terminal cell (which is 53–80 × 16–20μ), the broadest terminal cells usually with smaller elements connecting it with the cells of the hypodermium, the narrower ones being terminal members of a longer chain; all hyphae without clamp connexions.

Pluteus fibrillosus Murr. (Fig. 13)

The type from Chalmette, La., was collected by Earle (no. 129, NY). The specimen is in good condition and shows some white between the rather dense radiating and not quite straight fibrils which are rather deep coloured; margin now slightly sulcate on one side of pileus; stipe white. Spores 6–6·8 × 5·5–6·2μ, subglobose (very rarely globose); cystidia and cheilocystidia similar, cylindrical-ventricose or fusoid-subampullaceous, sometimes rather broad and short, others strongly elongated, numerous, hyaline to fuscidulous from an intracellular dissolved pigment, smooth and entire at apex, thin-walled, 52–66 × 8–18μ; epicutis of pileus consisting of bunches of fasciculate hyphae, with the basal septa of the terminal members nearly at an even level but the latter not equally long, often cystidioid, but extremely versiform, filled with fuscous intracellular dissolved pigment 27–115 × 9·7–15·3μ, broadly rounded at apex; basal tomentum present, consisting of hyphae without clamp connexions.

This is a good but apparently rare species of North America, near *P. subfibrillosus* Sing. and *P. rimosellus* Sing. from South America, and perhaps *P. hiatulus* Romagnesi from Europe (unknown to me).

Pluteus fibulatus Sing. in Sing. & Digilio

The type is at LIL and MICH. Nothing can be added to the diagnosis.

Pluteus flavofuligineus Atk. (Fig. 14)

The type from Coy Glen, N.Y. (CU) consists of a smaller and a larger carpophore; the larger one was analysed. Spores 6·8–7·8 × 5·5–6·5μ short-ellipsoid to ovoid; basidia 25–35 × 7·8–8·7μ; cystidia 43–100 × 12·8–40μ thin-walled, but sometimes with a thin melleous resinous incrustation, ventricose or more often ampullaceous, strongly staining from phloxine-KOH, with rounded-obtuse apex, but in most cystidia tiny nodulose or sterigmatoid appendages (up to 5 of them) present; cheilocystidia vesiculose, hyaline, e. g. 15·5μ broad, intermixed with cystidia and basidia, or only with cystidia; basal mycelium present, consisting of hyphae without clamp connexions; epicutis of pileus consisting of a loose interwoven fibrillose tissue with cystidioid terminal cells which may be strongly swollen

in comparison with the mother-cells, broadly cylindrical to subulate or more often ventricose, some extremely voluminous, filled with a pale ochre-hyaline sap, the apices sometimes slightly thicker walled than the sides and sometimes granularly incrusted, acute or forming a small neck, often subacute when tapering equally and gradually, often ampullaceous, sometimes with double apiculus (forked), 65–170 × 9–36 μ; hyphae without clamp connexions.

This seems to be extremely close to the European *P. leoninus* sensu Fayod, and *P. sororiatus* (Karst.) Karst. The brown-covered and venose to rugose or scrobiculate centre of the pileus differentiates the American species from *P. leoninus*, at least macroscopically, and the species described by Karsten (see also under *A. sororiatus*) seems to be plainly identical except for the slightly larger spores and the smooth disc, but this latter character does not appear to be absolutely constant unless it is permitted to assume that in the Caucasus where I collected *P. sororiatus*, two species exist side by side, one scrobiculate and the other smooth (see Singer, *Beih. Botan. Zbl.* II, **56**, 104, 1929), an assumption rather improbable since the rugose form has the larger spores characteristic of *P. sororiatus* rather than the smaller ones characteristic of *P. flavofuligineus*. Another most closely related species is *P. whiteae* (q.v.), and perhaps *P. melleus* (q.v.). Under the circumstances, I consider all these species forms of a single stirps, and, for the present purpose, leave them unchanged, i.e. as species—although future revisions might carry enough data to prove that at least some of them are merely forms or geographic races.

Pluteus floridanus Murr. sp.nov. (Fig. 15)

A *P. cubensi* (Murr.) Dennis differt sporis exiguis (5–6 × 4–5·5 μ) et stipite constanter albo. Ad truncos putridos, Florida. Typus in FLAS conservatus est.

Pileus 'sepia' to blackish fuliginous, squamulose-fibrous and tending to form rimose striations, with usually sulcate margin, dry, convex, then applanate or depressed with small but distinct umbo, 20–22 mm. broad. *Lamellae* sordid pink or pink, medium broad (2 mm.), crowded or close, free. *Stipe* pure white overall, glabrous, shining, naked, equal with a slight bulb or tapering upwards, about 30 × 1·5–2 mm. *Context* white, thin, unchanging, inodorous. *Spores* 5–6 × 4–5·5 μ, subglobose, few globose; basidia 25–30 × 7·5–8·8 μ, 4-spored; cystidia 52–55 × 8·5–16 μ, hyaline, ventricose-pedicellate below and ampullaceous above with broadly rounded apex, smooth; cheilocystidia varying from irregularly basidiomorphous to cystidioid (shape and size of pleurocystidia), hyaline, more crowded than the cystidia on gill edges; epicutis of pileus consisting of fibrils composed of elongate hyphae which are 3·5–15 μ broad and filled with intracellular dissolved or occasionally somewhat condensed pigment (fuscous), cylindrical to slightly clavate, sometimes with a slight constriction in the middle, with rounded tip; hyphae without clamp connexions.

On decayed mossy or earthy logs of frondose trees (*Quercus laurifolia*, *Coccolobis laurifolia*) in Florida, July until October. Alachua Co., Gainesville, 7 July 1938, W. A. Murrill (FLAS); Dade Co., Matheson Hammock, 4 October 1942, Singer F 959 (F).

Pluteus fuliginosus Murr. (Fig. 16)

Spores 6–7·5 × 4·3–6 (7·3) μ; basidia 4-spored; few 1–2–3-spored; cystidia ventricose below with an attenuate neck-like apex, the tip often nodulose or even forked or subramose, not pronged, with hyaline contents and wall, but sometimes some with a closely applicate resinous thin incrustation that makes them appear more yellowish in KOH than in NH_4OH, but also many hyaline cystidia seen with entire apices; cheilocystidia making the edge of the lamellae heteromorphous, all or most quite hyaline, shape of *Cervinus* metuloids, but not thick-walled and not pronged, intermixed with more vesiculose-mucronate cells, the latter about 20μ long, the former up to 70μ long, all about 9·8–18·5μ broad, with entire apex; epicutis of pileus consisting of chains of voluminous strictly elongate hyphae, the terminal members forming erect bunches of parallel cells which reach considerable length, and have up to 22μ in diameter, with pallid to pale umber dissolved pigment, hyaline, smooth walls, and acute or subacute tips; mycelium and carpophore hyphae without clamp connexions. This is the type from Lake Placid, Adirondack Mts., N.Y. (NY), no. 118. It is said to grow solitary. A fasciculate form of this was described by Murrill as *P. rhoadsii* Murr. from Florida (q.v.); it differs also in growing on oak rather than on coniferous wood. What may be a third form or race, or an extremely closely related species has been observed twice in Argentina:

Pileus strongly and densely umber fibrillose on white ground all over, or densely fuzzy and eventually radially fibrillose, showing, when dry, the pallid ground colour between the fibrils (s.l.), although not distinctly rimose with sulcate margin, convex then applanate, with umbonate or obtuse centre, 22–25 mm. broad. *Lamellae* pink, often with pallid edge, moderately close to close, 3–4 mm. broad, free. *Stipe* white, but lower half or at least basal region with umber or blackish fibrils, tapering upwards, 28–63 × 1·5–3 mm., base sometimes up to 7 mm. broad. *Context* white, unchanging, inodorous. *Spores* 6·2–7·5 × 4·8–6·5μ; basidia 22–26 × 7·8·2μ, 4-spored; cystidia ventricose below and ampullaceous or mucronate above, at edge also some ventricose-vesiculose or ampullaceous-subcapitate, hyaline, some with an inconspicuous stramineous resinous incrustation, with hyaline contents, numerous, 34–68 × 14–25μ, mostly 42–54 × 14–19μ; epicutis consisting of ventricose to cylindrical hyphal chains with evenly dissolved fuscous pigment, the terminal member fusoid to ventricose with strongly attenuate apex, with a thin subobtuse tip, 91–127 × 16·5–18·7μ; all hyphae without clamp connexions. On rotten wood, very shady and wet places in subtropical forest, Argentina, prov. Tucumán, Rio de los Sosas, between 1000 and 1200 m., Singer T 929 and T 2139, LIL.

This differs from the type form in becoming expanded at an earlier stage, in entire apex of the cystidia, and perhaps slightly smaller average size of the carpophores; it grows solitary, as the type form, and does not remind one of the Florida form (*P. rhoadsii*). After more knowledge on the distribution of the three forms has accumulated, it will probably become possible to distinguish them as geographic races (subspecies). *P. subgriseobrunneus* Murr., collected in the same region as *P. rhoadsii*, but solitary, grew on an undetermined 'dead log' and may therefore be considered as intermediate between *P. rhoadsii* and the type form (*P. fuliginosus*); it is larger than the Argentine form, but otherwise apparently identical with it.

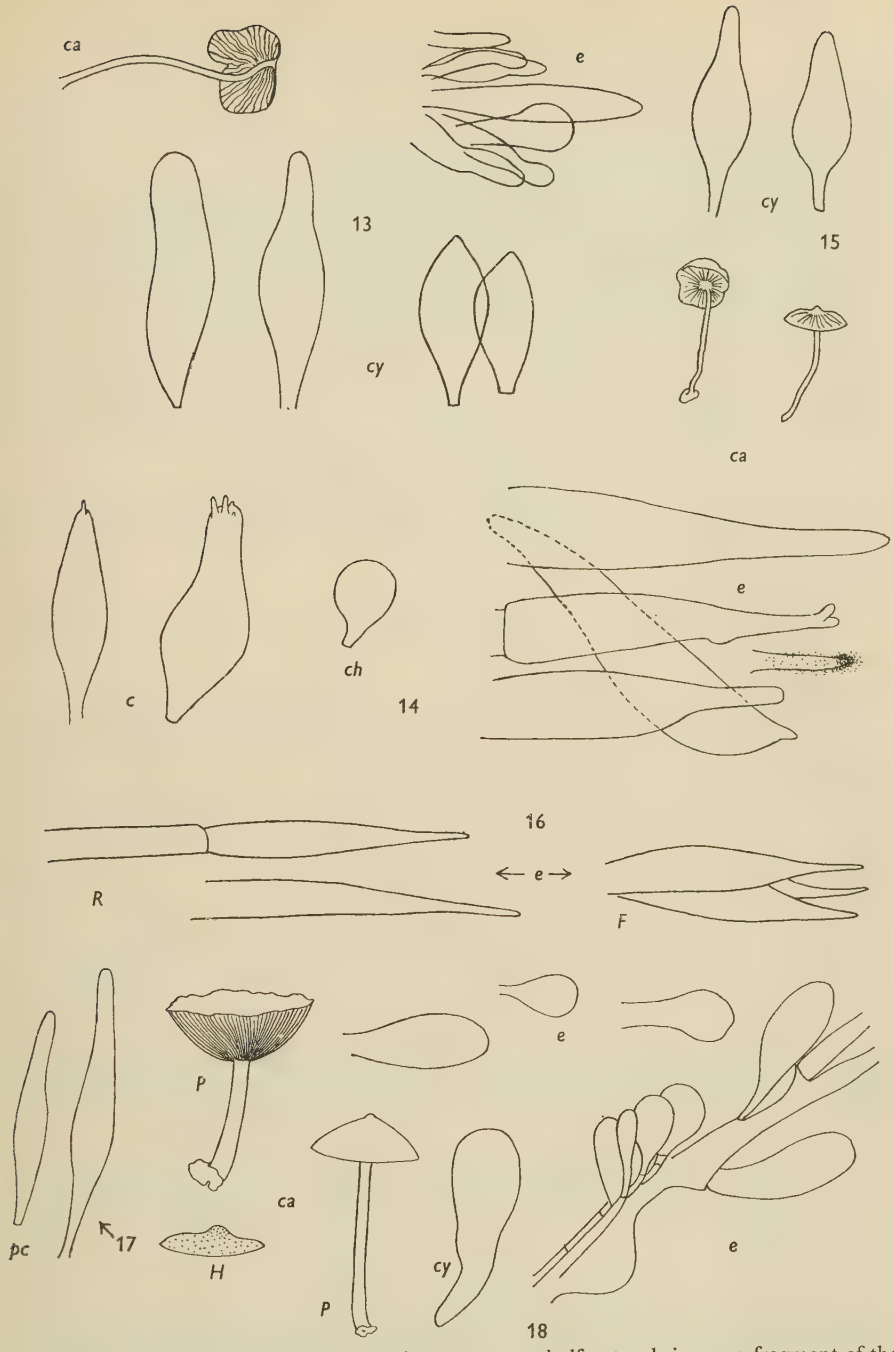


Fig. 13. *Pluteus fibrillosus*. *ca*, carpophore, from type, one-half natural size; *e*, a fragment of the epicuticular layer of the pileus; *cy*, pleurocystidia and cheilocystidia. All × 500.

Fig. 14. *Pluteus flavofuligineus*. *c*, cystidia of the sides; *ch*, of the edge of the lamellae; *e*, several terminal cells of the epicuticular hyphae of the pileus. All × 500.

Fig. 15. *Pluteus floridanus*. *ca*, carpophores (dried type material), one-half natural size; *cy*, pleurocystidia. × 500.

Fig. 16. *Pluteus fuliginosus*. *e*, (*F*), terminal cells of the epicutis of the pileus of the type of *P. fuliginosus*; (*R*) of the type of *P. rhoadsii*. All × 500.

Figs. 17, 18. *Pluteus glabrescens*. *pc*, pleurocystidia. × 500. *Pluteus glyphidatus*, *ca*, carpophores; (*P*) from painting of fresh type specimen, (*H*) from herbarium material (Kew), both in one-half natural size; *e*, structure of the epicutis of the pileus and (above) three cystidioid elements of the epicutis of the pileus; *cy*, pleurocystidium. × 500.

Pluteus glabrescens Murr. (Fig. 17)

Spores 6·5 × 5·4–5·7 μ; basidia 27–29·5 × 6·5–7·8 μ; cystidia not numerous, 49–74 × 14–20 μ, often slightly yellowish, crowded near edge (but there, as cheilocystidia, more polymorphous), on sides of lamellae more yellowish, ampullaceous to strongly ventricose below, and with a filamentous or conical-cylindrical 'neck' which may be nodose or even forked; epicutis of pileus consisting of long-ampullaceous-pedicellate terminal cells, about 4–11·5 μ in diameter, with melleous contents and obtuse tips (outside the disc); hyphae without clamp connexions. The pileus, under binocular, showing a yellowish fibrillosity, similar to that of *P. fuliginosus* and also appearing apparently slightly rugose-venose.

Earle, no. 1740, West Park, N.Y. 5 August 1903 (type).

This differs from *P. fuliginosus* in the colour of the young pileus and the pigment of the epicuticular cells which, moreover, are more obtuse than in *P. fuliginosus*.

Pluteus glyphidatus (Berk. & Br.) Sacc. (*Agaricus glyphidatus* Berk. & Br.) (Fig. 18)

A specimen in the Hoehnel Herbarium (FH) was misinterpreted by me. The species is not a true representative of the section Cellulodermi since the brown dots of the pileus of the type in both the Kew Herbarium and the British Museum consist of one or several central ascendant hyphae from which shorter (but not isodiametric) elements branch; these elements are vesiculose-elongate, fusoid with rounded apex, clavate, etc., and remain applicate or diverging at different angles in regard to the direction of the central hyphae of the 'dot', and often appearing on both sides of the central hyphae; these elements may be termed dermatocystidia, and are up to 39–44 × 13–17 μ, filled with a pale brown locally condensed pigment in the interior of the cells. The spores are 6·5 × 5·7–5·8 μ; the cystidia on edge and sides are clavated, broadly rounded and entire at the apex, hyaline and with a slight hyaline resinous incrustation (or without it); no clamp connexions observed. There is a picture at the British Museum which shows a strongly convex, then apparently depressed pileus, always with a small umbo, with brown small subverrucose dots at least in the centre, or else all over, in the first case with striate or sulcate margin, diameter to 40 mm.; stipe 35–45 × 2–5 mm., often with thickened base, this as well as the young lamellae and the ground colour of the pileus yellowish.

Pluteus granularis Peck (Fig. 19)

The box containing the type (NYS) also contains a coloured picture. The material includes material from Pine Hill and Worcester, N.Y. This is a common North American species, very close to the European *P. plautus*. The same species is also contained in the Atkinson Herbarium under the name '*Pluteus umbrisellus* Atk.' with a good photograph included. It was collected in abundance during the season of 1953 in Northern Michigan.

Pileus Partridge, Raw Umber (M. & P., R.), but with Pale (Olive-) Buff, ground colour (pl. 12 F 5, M. & P.) and deeper and brighter granules

which are usually denser on the disc and therefore the marginal zone usually paler, the umbo deeper coloured (Clove Brown, R.), sometimes the granules more pilose and so close that the pileus appears velvety, very frequently radially rugose in the centre, crenulate or fimbriate on margin, 34–60 mm. broad, conical-convex or convex and subumbonate, eventually applanate and depressed around umbo. *Lamellae* pink, but sordid pallid in youth, without discoloured edge, close or subclose, ventricose, up to 7 mm. broad, free. *Stipe* of the same colour and with the same covering as the pileus,

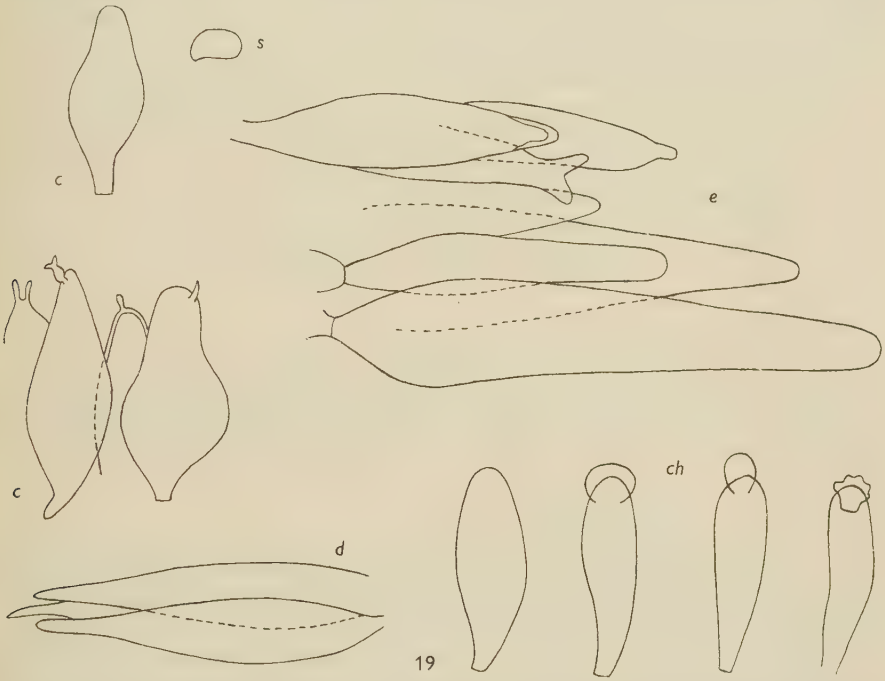


Fig. 19. *Pluteus granularis*. *c*, pleurocystidia, ×500; *s*, spore, ×1000; *e*, zone of the terminal members of the hyphal chains forming the epicutis of the pileus, ×500; *ch*, aberrant cheilocystidia from a collection from N.Y. (CU, 15168), ×500; *d*, dermatocystidia of the stipe, ×500.

or somewhat less, but never glabrous, somewhat paler or concolorous at apex, but never pallid, usually near 'Bister' (R.), stuffed, equal or slightly tapering up or downwards, 34–80 (125) × 3–7 mm. *Context* white, rather thin, inodorous but in age often foetid. *Spores* 5·7–7·7 × 4–5·7 μ, usually *c.* 6·5 × 4·8 μ, strongly elongated; basidia 22 × 6·8 μ, narrowed above, 4-spored; cystidia 35–68 × 10–36 μ, hyaline, but all or many filled with pale fuscous to fuscous cell sap, some with rather thick to thick walls, many with a pale melleous resinous applicate incrustation, usually fusoid to broadly ampullaceous, with rounded apex but often with 1–2 small simple or forked appendages (3·5–10·5 × 1·5–2·5 μ), wall 0·2–1 μ thick; cheilocystidia versiform, broadly ampullaceous, fusoid, clavate or broadly cylindrical, always with broadly rounded apex, but in some collections with the

same appendages as the pleurocystidia, in others with a strange globular appendage, mostly about 55μ long, 10–30μ broad, globose apical cell where present about 7–12μ diam.; epicutis of the pileus consisting of a trichodermium, split into fasciculate fragments, fuscous at least in the upper portion, few entirely hyaline, terminal cells fusoid, more rarely ampullaceous, or mucronate and some bifurcate, often some with the wall thickened overall or at the apex, apex rounded, 120–175 × 5–30 (70)μ, with evenly dissolved pigment, without incrustation; epicutis of stipe consisting of very similar hyphae but at least half of the terminal cells with subacute apex, all erect and forming a palisade, 9–18μ in diameter; hyphae without clamp connexions; hymenophoral trama inverse.

On very rotten logs and in hollow stumps (e.g. *Betula lutea*) in Eastern North America: *N.Y.*, type; and Cayuga Lake Basin, coll. Thom, Grim, Lewis, h.n. 15168, 18411, 18467 (CU); McGowan Woods coll. Jackson, h.n. 15286 (CU); Huntington Forest, Singer 199, FH. *Mich.*, Tahquamenon Falls, 29 June, 1953, Singer N 249 (F).

This differs from *P. plautus* (q.v.) in smaller spores and probably in colours. It may be considered as a subspecies of the European species.

Pluteus granulatus Bres.

I have not studied the type. The species is currently understood as corresponding to a rare species, close to *P. plautus* and *P. depauperatus* but with a beautifully brown (not fuscous) pileus and less strikingly granular stipe. Unknown to me, but may be very close to *P. glabrescens* Murr.

Pluteus harrisii Murr. (Fig. 20)

The type from Jamaica (NY), collected by Murrill and Harris is a species of the *Cervinus* group, with weakly horned metuloids and without clamp connexions. It is here redescribed:

Pileus Hair Brown with Chaetura Drab or Dark Vinaceous Drab centre, relatively dark coloured in most specimens, with smooth, then striate-sulcate margin, often very indistinctly subrugulose, convex, often subumbonate or subumbilicate, eventually applanate or slightly depressed, 20–45 mm. broad. *Lamellae* pink, subclose to close, subventricose, free, rather broad (up to 7 mm.). *Stipe* white, sometimes with pale greyish base, glabrous, naked, equal, shining, solid, 25–50 × 2–5 mm. *Context* white, thin, unchanging, inodorous. *Spores* 6–9·8 × 5–6·5μ; basidia 19–24 × 7–7·7μ, 4-spored; cystidia metuloid, rather numerous on both sides and edges, more numerous on sides of lamellae, hyaline, ventricose with concave upper outline, with thick wall (in upper half 1·5–2·8μ), gradually more thin-walled below (thin walled and easily collapsing in lower quarter), comparatively short and broad, ventricose with pedicel and a short neck, with broad, obtuse and low prongs, some metuloids with longer and the neck secondarily crested almost horizontal or recurved prongs, some with rather short erect prongs which are then relatively few (mostly 2), broad and broadly rounded at apex, but usually with (1)–3–4 (5) short (up to 4, but mostly up to 2μ long) prongs; 43–78 ×

14·3–26μ; cheilocystidia clavate-elongate, thin-walled, making the edge heteromorphous, intermixed with a few short-vesiculose-clavate ones, e. g. 33 × 18μ, hyaline, 33–42·4 × 7·8–18μ; epicutis of pileus consisting of applicate elongate hyphae, the terminal members subulate or ampullaceous or cylindrical, with gradually thinning but obtuse, or broadly rounded apex, the tips or the entire terminal cell usually hyaline, and 4·3–12μ broad below with fuscous, sometimes locally condensed intracellular pigment, especially in the lower cells of the chains, and there sometimes thicker (12·8μ), in average about 100μ long; hyphae without clamp connexions.

On burned woody matter of angiosperms and on decaying wood, Florida to Jamaica and Trinidad, fruiting almost the year round according to

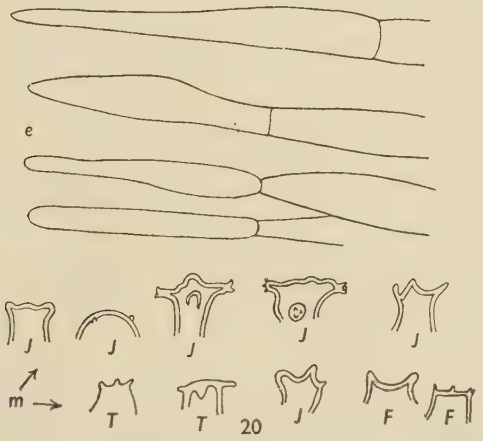


Fig. 20. *Pluteus harrisii*. *e*, terminal members of the hyphal chains of the epicutis of the pileus; *m*, metuloids (apical portion only), (*J*) type from Jamaica, W.I., (*T*) material from Trinidad, (*F*) material from Florida, U.S.A. All × 500.

climatic conditions: Florida, Highlands Hammock State Park, Highlands Co., 27 August, Singer F 413 (F); Jamaica, Troy & Tyre, Cockpit Co., no. 956, type (NY); Trinidad, St Joseph, bamboo plantation, 9 August, 1947, R. E. D. Baker 1495 (K), type of *P. cervinus* var. *bambusinus* B. & D. which is a synonym.

This species differs from certain forms of *P. xylophilus* in the definitely darker, and often smaller pileus, and the stipe which is usually white, or even if grey at base, never showing the distinct innate longitudinal fibrils of the Brazilian species; the spores are also somewhat larger on average, and the size of the fruiting bodies slightly smaller. In *P. xylophilus*, in addition, one always observes a large number of normally pronged metuloids (as in typical *P. cervinus*) and only in some carpophores the poorly pronged metuloids of the type of *P. harrisii* occur in the region of the edge.

Pluteus haywardii Sing., see under *Agaricus alborubellus* Mont.

Agaricus hispidulus Fr.

A type specimen is not preserved. The complex *P. hispidulus-exiguus* has been restudied by Kühner & Romagnesi (1953), and their results are here accepted as the most probable solution available. Consequently, *P. hispidulus* var. *microsporus* Dennis is here treated as an independent species, **P. microsporus** (Dennis) comb.nov. (*P. hispidulus* (Fr.) Quél. var. *microsporus* Dennis, *Bull. Soc. mycol. Fr.* **69**, 155, 1953).

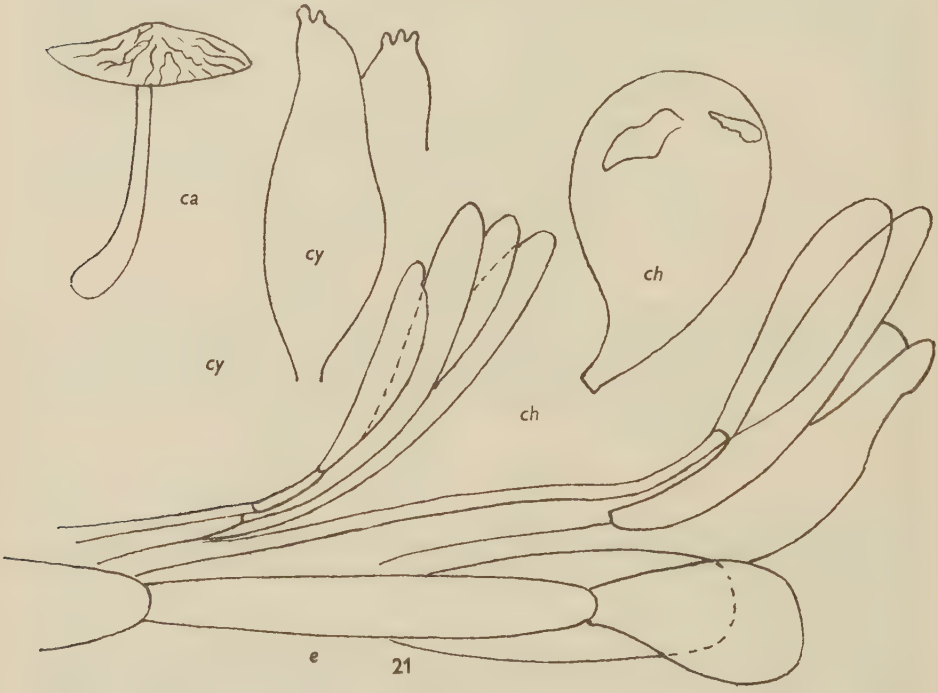


Fig. 21. *Pluteus jaffueli*. *ca*, carpophore, natural size; *e*, structure of the epicutis of the pileus, × 500; *cy*, pleurocystidia, × 1000; *ch*, cheilocystidium, × 1150.

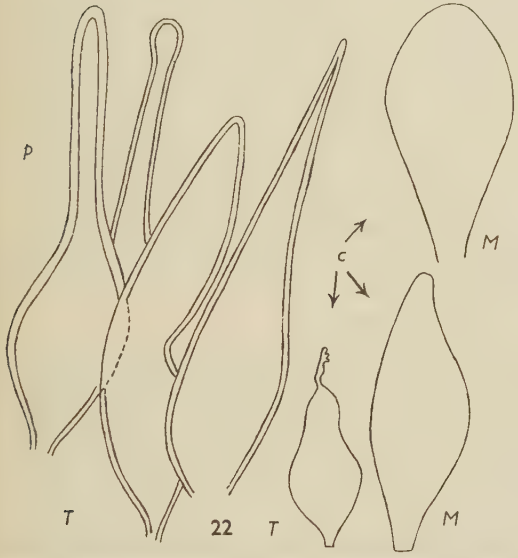
Pluteus jaffueli (Speg.) Sing. (*Mycena jaffueli* Speg.) (Fig. 21)

The description and generic determination of this species are both extraordinarily misleading, but the type is identical with *P. defibulatus* Sing. which, in turn, is extremely close to *P. umbrosus* (q.v.). Compare also *Sydowia*, **8**, 123, 1954, where the new combination *Pluteus jaffueli* (Speg.) Sing. was proposed.

Pluteus latifolius Murr. (Figs. 22, 23)

The type from Seattle, Wash. (NY) looks somewhat like *P. cervinus* when dried, with very broad lamellae. Under a dissecting binocular, the surface of the pileus appears tomentose-fibrillose, especially in the centre which is

said to have been rugose when fresh. The edge of the lamellae is not discolorous. The stipe is characteristically fibrillose from erect concolorous fibrils, especially below. Spores 5·5–6·8 (7·7) × 5–5·5 (6·5) μ; basidia mostly destroyed. Cystidia little evident now, but certainly not of the metuloid type, some seen to be ampullaceous, one with appendage, melleous from a melleous resinous incrustation, but not fuscidulous from dissolved pigment, e. g. 44 × 18·5 μ. Structure of the epicutis definitely not cellular; fibrils of the base of the stipe consisting of chains of hyphae with cystidioid terminal members, the latter e. g. 92–155 × 15–24 μ, ventricose



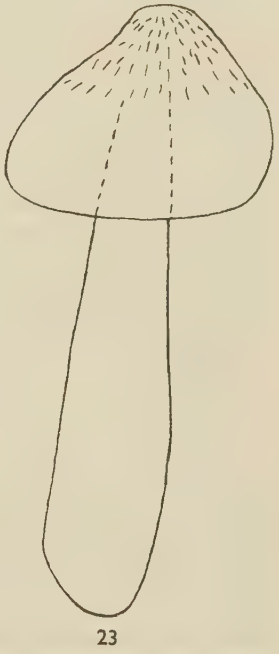


Fig. 22. *Pluteus latifolius*. *c*, pleurocystidium, × 500; *p*, elements of the pilosity of the stipe, × 500. *T*, from type; *M*, Michigan material.

Fig. 23. *Pluteus latifolius*. Carpophore, × 1.

at base and attenuate upwards to an acute or more frequently obtuse tip, sometimes subcapitate at apex, with a dissolved pale brown sap in many cells, more rarely hyaline, with thick wall (1–2 μ); all hyphae without clamp connexions.

A similar fungus was collected by the author in Michigan, Douglas Lake, Cheboygan Co., 22 June 1953. The primordia of 1 mm. diameter are brown with pallid margin and show this species to have hemiangiocarpous development. Later, the pileus becomes campanulate-convex, umbonate, with ochraceous brown fibrillose squamules in the centre, and whitish fibrillose squamules in a middle zone, finer white flocculose at the margin. The lamellae are pink before the spores have matured. The stipe tapers upwards and is entirely covered by rough pallid to whitish fibrils

on a ground which is white above and pale brownish below; the base itself is whitish woolly. The context is white and odourless. In this specimen it was possible to observe the hymenial cystidia more carefully; they were clavate to ventricose or ventricose-ampullaceous, hyaline, smooth, with thin walls, 60–74 × 21–33 μ.

I am convinced that this and the type of *P. latifolius* are conspecific, the latter being a more advanced state of the former. Both grew on frondose wood. The Michigan collection is preserved at F.

Pluteolus leaianus Berk. ex Cooke in Sacc.

The type from Ohio, U.S.A. (K) is a species of the *Pluteus cervinus* type. The spores are 6·5–9 × 5·3–6 μ; metuloids thick-walled, of the type encountered in typical *P. cervinus*, and the hyphae have no clamp connexions. The terminal members of the hyphal chains forming the epicutis of the pileus are long-fusoid to subclavate and very elongate, filled with umber brown dissolved pigment and showing rounded tips.

This species is undoubtedly a *Pluteus* and not a *Pluteolus* (= *Bolbitius*), and apparently a synonym of *P. cervinus* since it has the same metuloids and rather large spores which, in the region from where it came, may only be encountered in typical *P. cervinus*. It seems incredible that as late as 1895, this common European species should have been described as a new species of *Pluteolus* by a European author.

Another species belonging in the same group, and misdetermined as far as its genus is concerned, is *Agaricus lilacinus* Mont.

The type of *A. lilacinus* Mont., collected by Sullivant near Columbus, Ohio, (PC), is likewise of the *Pluteus cervinus* type. It seems that the colour indicated by Sullivant was misleading enough to suggest affinity with *Mycena pura*, in spite of the fact that the horned cystidia (metuloids) were correctly observed by Montagne. The spores are 5–7·2 × 3·5–5·7 μ. They are, consequently smaller than in typical *P. cervinus*. There is no dimorphism as far as the metuloids are concerned, and the cheilocystidia were not recognizable in the type specimens. This seems to be identical with American specimens of what I determined as *P. cervinus* var. *minor* Sing., differing from the European type of the variety in some small characters such as the fuliginous innate fibrils of the stipe which, consequently, is not white, and coinciding with the type of var. *tucumanensis* Sing. in Sing. & Digilio in this regard. If this form is considered as a species, it becomes necessary to accept Montagne's epithet in spite of its erroneous implication.

North American collections of this fungus are characterized as follows:

Pileus Malay, Cocoa Brown, with the centre near Cracker (M. & P.), subhygrophanous, subsmooth, subfibrillose, with very short marginal transparent striation, convex, then applanate, umbonate, 34 mm. broad. *Lamellae* pink, rather broad, free. *Stipe* white but with fuliginous longitudinal innate fibrils slightly darkened, with white apex, 41 × 3·5–4 mm. *Context* white, unchanging, thin, inodorous. *Spores* 5–7·5 × 3·5–5·5 μ; basidia 4-spored; metuloids only of one type, ventricose ampullaceous or fusoid with slightly concave outline at apex, with medium high subacute to subobtuse mostly simple erect prongs, with moderately thick to rather

thick walls in the upper third or half, size as in *P. cervinus*, hyaline; cheilocystidia vesiculose or vesiculose-short-clavate; epicuticular hyphae as in *P. cervinus*; hyphae without clamp connexions.

On dead wood of *Tsuga canadensis* and probably also other trees fruiting in summer. U.S.A. *Ohio* (type); *Mich.*, Maple River, Emmet Co., Singer N 894 (F).

Pluteus lepiotiformis Murr.

Spores of the type (from Louisiana, Earle 74, NY) 5·5–6·5 × 5·5–6·2 μ, almost geometrically globose; cystidia not recovered; epicutis of pileus consisting of elongated cells with evenly dissolved fuscous intracellular pigment. The holotype is merely a small fragment.

Earle 124, also determined *P. lepiotiformis* and evidently a paratype collected 2 days later in the same state (Chalmette, La.), shows more details than the holotype; here, the terminal cells of the hyphal chains forming the epicutis (the hairy spinules in the centre) are broadly rounded toward the apex, and tapering toward the next-lower cell, forming erect hyphal bunches, filled with intracellular dissolved pigment; hyphae without clamp connexions.

This has somewhat the aspect of the European *Pluteus hispidulus* from which it differs in the shape of the terminal hyphae of the pileus and the almost geometrically globose spores. However, it is apparently very little different from and probably a synonym of *Pluteus nitens* Pat. (q.v.).

Pluteus leoninus (Schaeff. ex Fr.) Quél. (*Agaricus leoninus* Schaeff. ex Fr.)

Although there is no type, apart from the diagnosis by Fries, 1821, I interpret this species in the sense of Konrad & Maublanc, Kühner & Romagnesi, and other European mycologists, following the first interpretation by Fayod. This, according to notes taken from material from Eastern Europe and the Caucasus, has spores as indicated by Kühner & Romagnesi usually nearer the lower limits, basidia 34 × 7·4 μ, 4-spored; cystidia 52–78 × 12·5–28·5 μ, fusoid to cylindrical-fusoid, some with somewhat ampullaceous apex, others with acute apex, but more with rounded tip, hyaline, smooth; epicutis of pileus consisting of ascendant hyphal bunches which become appressed, the terminal members ampullaceous to fusoid-ventricose, with attenuate and usually subacute to acute tip, very large: 110–180 × 25–33 μ. The pileus is not rugose in the centre, yellow with brownish ochraceous umbo with striate margin; stipe more or less yellow.

Agaricus lilacinus Mont. see *A. leaianus*

Pluteus luteomarginatus Rolland

According to the descriptions available, this seems to be extremely close to *P. sororiatus*, perhaps identical with it, although it is said to have slightly smaller spores. The habitat on conifers does not seem to be constant since I observed *P. sororiatus* on both coniferous and frondose wood.

Pluteus magnus McClatchie (Fig. 24)

The type from San Francisquito Creek, California (UC, CI) has metuloid cystidia of a type different from those of *P. cervinus*, viz. fusoid with conical portion above the thickest region, tapering to a point and either simple or forked at the apex, with lateral spinules in the upper third or half, few without such spinules, with moderately thick wall (0·5–1 μ), 67–81 × 13–20 μ; spores 6·5–8·7 × 4–5 μ; basidia 27·5–36 × 7·5–7·8 μ, 4-spored; epicutis of elongated hyphae; hyphae without clamp connexions. The stipe is white, solid, the pileus is slightly fuscous, pallid on the margin with more greyish centre. Carpophores very large.

Similar specimens have been collected by the author in the East of North America:

Pileus white, to very pale isabelline-umber, with or without fuliginous appressed fibrillose squamules in the very centre, the margin opimous-subviscid, the centre smooth, sometimes faintly innately fibrillose all over, and eventually sometimes splitting radially as some Inocybes, sometimes somewhat scrobiculate, convex-subumbonate, eventually irregularly applanate and sometimes subumbilicate, 70–105 (180) mm. broad. *Lamellae* white, soon pink, with pink edge, sometimes slightly eroded at the edge or with entire edge, broad, close to crowded, free. *Stipe* pure white or very slightly innately fuliginous fibrillose at the base, sometimes slightly but coarsely longitudinally fibrous-rugose, equal or with thickened base, solid, 65–90 (200) × 6–20 (24) mm. *Context* white, unchanging, inodorous. *Spores* 5·4–8·7 × 4–5·8 μ, either very small or very elongated (or both); basidia 27·5–28·5 × 6·5–7·8 μ, 4-spored; metuloids fusoid with narrow neck or more often gradually tapering to an acute or forked apex, with or without (always some metuloids with) lateral spinules in the upper half, broadest below or in the middle, with wall 0·5–1·2 μ thick at least in upper portion, all (lateral and apical) spinules acute, all metuloids hyaline, 49–81 × 10–20 μ; cheilocystidia hyphous to elongate-clavate, with protoplasmatic contents or 'empty', never vesiculose, or only seemingly so (because of a secondary septum), with rounded-obtuse apex, 32–180 × 7–14·5 (16) μ; epicutis of pileus consisting of chains of filamentous hyphae, the terminal member often subulate, or ventricose or ampullaceous, repent, the apex, tapering to a subacute to rounded thin tip (in the subulate and ampullaceous cells apex 3–3·7 μ diameter), broadest portion 5–11 μ in diameter, with dissolved fuscous pigment when taken from the central region of the pileus; hyphae without clamp connexions.

Growing solitary or in small groups on dead frondose wood, also on buried and burned wood, on dicotyledonous trees (*Alnus*, *Quercus*), fruiting from April until fall; *Vt.*, Grand View Mt., coll. Burt, det. Peck (as *P. tomentosulus* Peck, *ex errore*), FH; *Mass.*, Purgatory Swamp, Singer, July 1941 (FH); *Fla.*, Alachua Co., Sugarfoot Hammock, F 1667c (F), Gainesville F 1756a, Payne's Prairie, F 1798 all coll. R. Singer (F); *Ill.*, Geneseo, July 1898, E. T. & S. A. Harper, no. 57 (F); *Calif.*, type.

This species has frequently the aspect of *P. curtisii*, from which it differs in the elongated cheilocystidia and the complete absence of metuloids of the *Cervinus* type, i.e., the metuloids are monomorphic.

In Florida, there is also a similar form which, however, differs in strikingly aberrant habit, viz. long and thin stipe and small pileus, e. g., pileus 27 mm. broad, stipe 83 × 5·5 mm., and by uniformly fuscous pileus. According to the description, one would be inclined to think that *Pluteus australis* Murr. is this small form or species, but I have seen no authentic material. My own material came from Newnans Lake, Alachua Co., Fla., 19 April 1953, Singer F 1859, F. I insert this form tentatively under *P. australis* in the key.

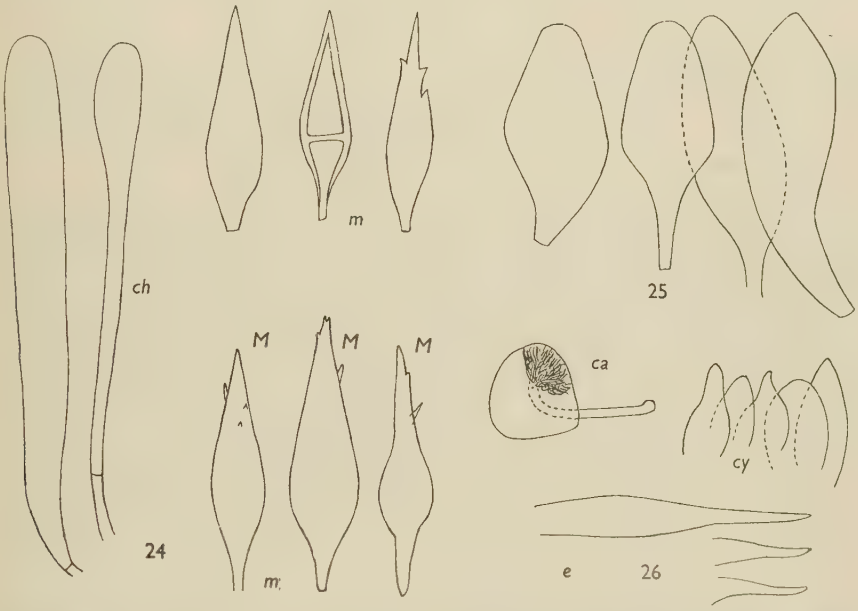


Fig. 24. *Pluteus magnus*. *ch*, cheilocystidia; *m*, metuloids, (*M*) from the type collection of *P. magnus*. × 500.

Fig. 25. *Pluteus multistriatus*. Cystidia, × 500.

Fig. 26. *Pluteus nigrolineatus*. *ca*, carpophore of dried specimen (type), half natural size, with the pileus seen from above (fibrillose lines of surface only indicated in upper right quarter), half natural size; *cy*, cystidia, × 500; *e*, epicuticular elements (terminal members, from pileus of type specimen), × 500.

The California form differs only in being somewhat larger than the specimens from the East, although these latter collections are all remarkably large for the genus; they have likewise slightly smaller spores, but the difference does not seem significant since the majority of the spores of the type are as those observed in the Eastern form. The more coloured (pale umber margin) and the almost white forms occur both in the East, sometimes side by side in a single collection and rising from the same mycelium. This is the only case known to me where a *Pluteus* of the *Cervinus* group varies in this way (excepting rare albino forms of ordinarily well-pigmented species).

Pluteus melleus Murr.

The only authentic collection is the type (NY) which consists of a fragment of a carpophore and is not in very satisfactory condition. Spores 6·5–7·4 × 5·3–6 μ; cystidia present, not of the *Cervinus* type (not metuloid); epicutis of pileus not cellular. The colour of the surface of the pileus is still melleous; the lamellae are broad.

Unless topotypical material can be collected that proves this species to be sufficiently different, I should suggest that it is a form or variety of *P. flavofuligineus*.

Pluteus minimus Henn.

The type has been destroyed. We have, however, one collection from north-western Argentina which agrees with Hennings's description. It is therefore tentatively determined as *P. minimus* Henn.:

Pileus squamulose-fibrillose, the fibrils very deep brown ('Biskra' M. & P.), slightly sulcate, convex, 2–6 mm. broad. *Lamellae* white, then pink, broad, ventricose, moderately close, free. *Stipe* hyaline, equal, glabrous, 6–15 × 0·2–0·8 mm. *Context* white, inodorous, thin. *Spores* 6·2–7 × 5·5–6·2 μ, between globose and subglobose, smooth, stramineous; basidia remarkably large, 27–34·5–8·5 × 9·5 μ, 4-spored, some with mucronate apex, cystidia on sides of lamellae not observed; cheilocystidia present, hyaline, vesiculose, some with crystals at apex, e. g. 37 × 17·8 μ; trama of the hymenophore inverse; epicutis of the pileus not cellular, the squamulae consisting of palisades or erect dermatocystidia which are between the squamulae repent and scattered; dermatocystidia of the squamules of the pileus subulate with narrowly attenuate and subacute to subobtuse thin tip, with brownish dissolved pigment evenly distributed in the interior of the cells, these 80–100 × 17·5–23·3 μ.

Parque Aconquija, Sierra de San Javier, prov. Tucuman, 1 April 1949, Singer T 359 (LIL), growing on a moss-covered living trunk of *Phoebe porphyria*.

Apparently rare in South America. Only once observed, and at first mistaken for *P. cubensis*.

Pluteus multistriatus Murr. (Fig. 25)

The type from Mexico (NY), W. A. & Edna Murrill, no. 111 is in rather good condition. Spores 6·5–7 × 4·8–5 μ, relatively elongate; cystidia on sides and edges not numerous, hyaline with fuscous condensed (gelatinous) pigment bodies inside, broadly ventricose to broadly clavate, often broadest below and gradually attenuate but tip always very broadly rounded, 55–110 × 16–25 μ; epicutis of pileus made up of radial fibres consisting of more or less parallel hyphal strands, many with fuscous intracellular pigment, repent and smooth, not acute; all hyphae without clamp connexions. The pileus appears to be radially striped and sulcate (pallid and fuscous sectors alternating), but not radially rimose or plicate in the manner of the Coprini or Inocybes.

This seems to be a good and characteristic species. Murrill's paratype (No. 112) from the same station and of the same date, is deposited as a depauperate form, but seems to be less valuable material of the same species.

Pluteus murinus Bres.

This species is unique in Europe, although rather closely related to similarly radially fibrillose species in the tropics. It has been found by Kühner and Romagnesi who key it out in their *Flore Analytique*, and good material was also collected by Vasilieva in the Western Caucasus (LE, KAZ), where the terminal members of the epicuticular hyphae are long-fusoid with brown dissolved intracellular pigment, tapering to a thin but not acute tip, 100–120 × 10–12 μ; cystidia fusoid and often with thin apical mucro; cheilocystidia without mucro.

Pluteus myceniformis Murr.

The type from Jamaica, W.I. (NY) is in rather good condition. Spores 7·3–8·8 × 6·5–7 μ, cystidia numerous on edge and sides of lamellae, hyaline, always broadly rounded above, versiform, about 50–55 × 15–22 μ; epicutis of the pileus consisting of elongated hyphae, in the centre with plaques of brown pigment, terminal cells usually very broad at the apex, rarely attenuate or subacute or capitate at the apex. Pileus now pale yellowish, almost rusty in the centre, margin whitish, somewhat sulcate in dried condition. The habit is indeed somewhat mycenoid as the name implies. The lamellae are whitish, subclose, free.

This is probably a distinct species, similar to *P. niveus*.

Pluteus nigrolineatus Murr. (Fig. 26)

The type from Gainesville, Florida (FLAS) has spores 6–10 × 4·7–7·4 μ; cheilocystidia numerous, versiform, often vesiculose or broadly fusoid, either acute or rounded at the tip, not appendiculate, hyaline, 52–67 × 12–17 μ; cystidia similar, more fusoid; cuticle of pileus consisting of elongate hyphae exclusively, semierect terminal hypha fusoid, very long (reaching 300 μ and more) 10–15 μ thick, attenuate at apex into a filiform acute or subacute tip; hyphae of the stipe with clamp connexions.

It seems that in Europe, the current interpretation of *P. cyanopus* is that of a species with a cellular epicutis. Thus, in spite of the fact that this rare species is represented only by one collection of certain identity, and that not in very good condition, it should be recognized as a valid species of *Pluteus*. The pileus is now rather flat and looks fibrillose, the fibrils radiating more or less on sordid-greyish ground; on the base of the stipe, dark lines are visible. Another collection (F 9375) looks more like a broader, short-stemmed form of *P. floridanus*, and is probably not identical with the type.

Pluteus nitens Pat. (Fig. 27)

The type from Mexico, est. de Veracruz, 19–29 February 1891 (FH), is accompanied by a coloured picture which shows the pilei short-striate, in one carpophore slightly crenulate, convex, obtuse, and with 'café au lait' colour, in others slightly more olive brown and the stipe not pure white. Pileus 17–28 mm. broad; stipe 12–26 × 1–1·5 mm., base 2–3 mm.; lamellae 3·5–4·5 mm. broad. The specimens show the surface of the pileus characteristically finely-fibrillose-pilose, on the disc almost punctate in some, towards the margin rimulose as in *P. murinus*, not strongly radially rimose or pectinate, but the white flesh showing s.l. between the tiny fuliginous fibrils, margin now short-sulcate. The original notes of the collector say: 'Sur tronc d'arbre. Chapeau café au lait foncé, luisant, finement strié radialement et circulairement; feuillets café au lait jaunâtre. . . Pied blanc sale, glabre, luisant. . . .' I interpret the striations indicated here as referring to the direction of the fibrils. Spores 5·5–6·5 × 5·2–6 μ, from as globose as 6·5 × 6·5 μ to subglobose (6·5 × 5·7 μ), i.e. geometrically globose to subglobose; hymenial structure poorly showing, but there do not appear to be brownish cystidia; hyphae not checked for clamp connexions; epicutis of pileus of elongate elements, according to Patouillard's drawings (probably made when the specimens were in better condition) 'repent', fusoid to cylindrical with broadly rounded tips and cystidia of hymenium fusoid with broadly rounded tip, 49 × 20 μ.

This has essentially the characters of *P. lepiotiformis* Murr. (q.v.), and I believe the two species to be the same or at least forms of the same species. This species would indeed be rather close to *P. hispidulus* as stated by Dennis, but a number of characters distinguish it from the European species. I have no personal collections of this.

On the other hand, we have collected, in Argentina, a specimen which keys out with *P. nitens* although I identify it with this species not without some hesitation. It is not only smaller but shows distinctly blackish bordered gill edges and dark dots on the sides of the lamellae when seen fresh under a binocular; the dark edge remains visible on dried material under a binocular; however, the cheilocystidia and pleurocystidia are hyaline or subhyaline under oil immersion (KOH, NH_4OH, and chloral hydrate mounts) so that it must be assumed that the scattered pigment bodies, especially at the edge, cause the discoloration of the cystidia intercellularly.

Pileus finely dark pruinate on whitish ground, pruinose particles very crowded and pileus Conga to Piccadilly, later slightly sulculate, not transparently striate, subumbonate, depressed around umbo, otherwise convex, 6 mm. broad. *Lamellae* greyish white, blackish bordered, broad, ventricose, sinuate-free. *Stipe* whitish hyaline, fresh with a slight fuliginous appressed fibrillosity which disappears in dried material, equal, 14 × 1–1·2 mm. *Context* white, inodorous. *Spores* almost geometrically globose, 5·5–6·7 × 5·3–6·5 μ; basidia 4-spored, 22·7 × 8 μ; cystidia on edge and sides varying from ampullaceous to cylindrical, rarely subcapitate, subhyaline or hyaline, some granular inside, thin-walled, 34–38 × 8–9·5 μ; cheilocystidia similar, numerous; intercellular brown pigment bodies scattered

in hymenial preparations; epicutis of elongated hyphae with rounded apex in the terminal members, these about 10μ in diameter and with evenly dissolved fuscous pigment; all hyphae without clamp connexions.

On rotten wood, very humid and shady place, subtropical forest, 4 February 1955, Singer T 2137 (LIL), Rio de los Sosas, prov. de Tucumán.

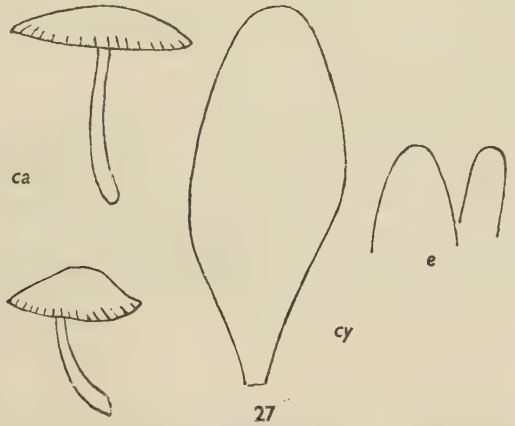


Fig. 27. *Pluteus nitens*. *ca*, fresh carpophores of type, × 1; *cy*, pleurocystidium, × 1000; *e*, apices of terminal members of epicuticular hyphae of pileus. × 1000.

Pluteus niveus Murr. (Fig. 28)

The type from West Park, N.Y. (NY) was collected by Earle, and appears to be identical with one of my collections determined, originally, as *P. roberti*. But since the interpretation of the latter species in Europe has become so difficult that it was abandoned by Kühner & Romagnesi, I do not wish to complicate matters by giving the Friesian species a new interpretation, although there are good reasons to think that *P. niveus* is closest to what Fries must have used as model for his illustration. Further studies of the type locality in Sweden might throw some additional light on this problem. *P. exiguus* may be a less glabrous form of this species.

Pileus white, ochraceous or light brown because of minute appressed fibrils in the centre of some caps, in others entirely white, not viscid, convex and subumbonate to umbonate, later becoming more applanate, 20–28 mm. broad. *Lamellae* white, then pink with white edge, finally entirely pink, subclose, broad, ventricose, free. *Stipe* pure white but middle portion sometimes with very pale brownish appressed fibrils like the centre of the pileus, solid, equal, 26–46 × 2–4 mm. *Context* white, unchanging, thin, inodorous. *Spores* 6·5–8·7 × 5–6·5μ; basidia 7–7·7μ broad, 4-spored; cystidia ampullaceous, usually not very numerous, 40–66 × 12–20μ; hyaline, rarely broadly fusoid with two apical mucros, both long and thin, some with a very thin melleous resinous incrustation (in herbarium material); cheilocystidia similar, usually ampullaceous, i.e. ventricose-fusoid with relatively short thin neck or mucro, 58–73 × 14·5–19·5μ; epicutis of pileus of elongated hyphae, the terminal member usually very

voluminous, those of the centre sometimes filled with a melleous cap, otherwise all hyaline; all hyphae without clamp connexions.

On sandy soil and earth under frondose trees, most frequently *Fagus grandifolia* (and possibly *Quercus*), fruiting in August and September. U.S.A., N.Y., type. Adirondack Mts., Huntington Forest, Singer 177 (as *P. roberti*), FH.

Pluteus patricius (Schulz. in Kalchbr.) Boud. (*Agaricus patricius* Schulz. in Kalchbr.) (Fig. 8)

The type consists merely of the picture published by Kalchbrenner in *Icones Selectae Hymen.* **1**, 20, pl. 10, fig. 2, 1873). However, this figure is excellent, and permits the identification of this species with the only European species of this habit and colour, *A. curtisii* Berk. I have studied numerous European collections (see under *A. curtisii*); only that of Cooke on oak stump, Coventry, Adams 1885 (K) is incorrect and belongs in *P. cervinus*. Cooke's picture shows what might pass as *P. curtisii* but may not be a true illustration of the collection on which it was allegedly based.

Pluteus pellitus (Pers. ex Fr.) Kummer (*Agaricus pellitus* Pers. ex Fr.)

The first correct and at the same time precise interpretation of this species was given by Kühner & Romagnesi, who recognize this as a pure white species with horned metuloids and clamp connexions. There is, however, in Europe, also a species without clamp connexions which I have not so far studied very carefully. A specimen of this from Strupets near Vratsa, Bulgaria, on worked oak wood, 15 August 1924, coll. B. Barzakoff no. 3 (K), has normally hooked metuloids, but no clamp connexions. This may be *P. viscidulus* (q.v.).

Pluteus petasatus (Fr.) Gillet (*Agaricus petasatus* Fr.) (Fig. 29)

The only species corresponding completely to the original description given by Fries is represented by a collection from Halesworth, Suffolk, on sawdust, 9 June 1931, which is in excellent condition (K). The pileus is umbonate, glabrous, very pale umber, finely radially striate up to the centre by innate fibrils. The stipe is slightly innately floccose to fibrillose on one side. Pileus 55 mm. broad; stipe 110 × 8 mm. What may be the same species was described by Métrod (*Rev. Mycol.* **8**, 12, 1943) as *Pluteus cervinus*, 'forme à pied pelucheux'.

The microscopical data obtained from the above-mentioned British collection prove that this species is not merely a form of *P. cervinus* (unless one prefers to combine the entire *Cervinus* complex into one macrospecies) but an autonomous, rather rare species: Spores 5·5–7·3 × 3·8–5·8 μ; metuloids fusoid, entire or with bifid tip, without lateral spinules, not numerous, with thin to thick (1 μ) wall, thickest in the middle and tapering equally towards base and apex, with subacute to acute apex if entire, e. g. 88 × 18·8 μ; cheilocystidia dimorphic, some (form 1) almost exactly as the metuloids but constantly thin-walled and more variable in size and shape,

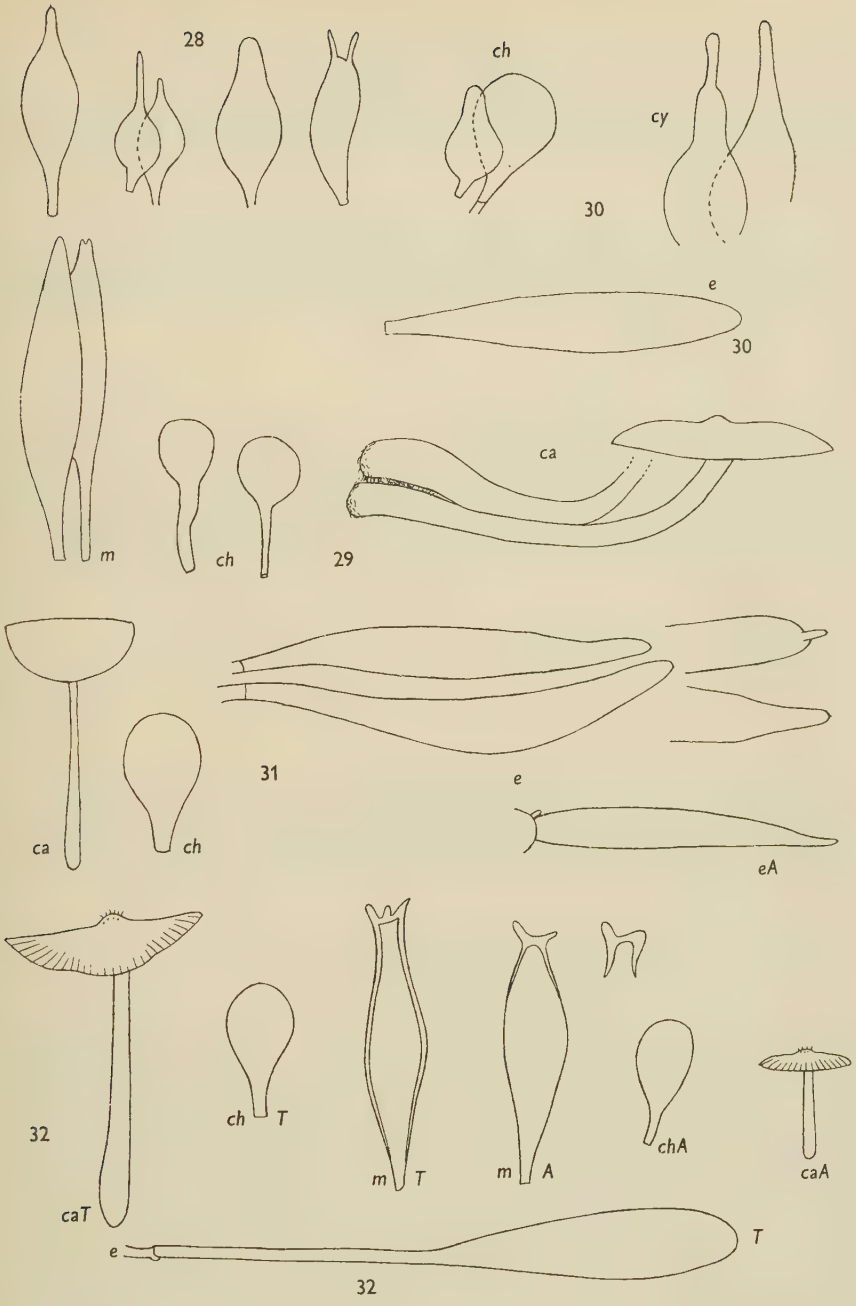


Fig. 28. *Pluteus niveus.* Cystidia, × 500.

Fig. 29. *Pluteus petasatus. ca*, carpophores, one-half natural size; *ch*, cheilocystidia; *m*, metuloids. All × 500.

Fig. 30. *Pluteus rimosellus. cy*, pleurocystidia, × 500; *ch*, cheilocystidia, × 450; *e*, terminal cell of epicuticular hyphae of pileus, × 450.

Fig. 31. *Pluteus roseipes. ca*, carpophore, one-half natural size; *ch*, cheilocystidium, × 500; *e*, terminal cells of epicuticular hyphae of pileus, × 250.

Fig. 32. *Pluteus salicinus. caT*, carpophore of the typical form, × 2; *chT*, cheilocystidium of the typical form; *mT*, metuloid of the typical form; *mA*, metuloid of var. *achloes*; *chA*, cheilocystidium of var. *achloes*; *eA*, terminal cell of the epicuticular hyphae of the disc in var. *achloes*; *caA*, carpophore of var. *achloes*, one-half natural size; *eT*, terminal cell of the epicuticular hyphae of the marginal zone in the typical form. All details × 500.

others (form 2) globose and long-pedicellate, the apical globule about 15μ in diameter; epicuticular hyphae elongate, repent; all hyphae without clamp connexions.

Pluteus plautus (Weinm.) Gillet (*Agaricus plautus* Weinm.)

A type could not be discovered in LE, but the species as generally understood by European mycologists does occur in the region where Weinmann collected, cf. Métrod, l.c.

Pluteus rhoadsii Murr.

The type from Florida (FLAS, FH, NY) was distributed in a fairly large number of carpophores, but many of them are sterile or too young to produce many mature spores. The spores recovered measure 5·8–6·3 × 4·8–5·5μ (NY). All other characters are in perfect agreement with those of *P. fuliginosus* Murr., and the two species are, in my opinion, synonymous.

Pluteus rimosus Rick.

There are no type specimens. This is a nomen dubium, and a homonym of *P. rimosus* Murr.

Pluteus rimosellus Sing. (Fig. 30)

Nothing can be added to the diagnosis given in the original publication. This seems to be very close to the European species *P. hiatulus* Romagnesi in Kühn. & Rom. nom. subnud.

Agaricus roberti Fr., see under *P. niveus* Murr.

Pluteus roseipes Höhnel (Fig. 31)

The type (FH) from the northern slope of Puchberg (Austria) has now pale umber to grey-brown pileus with a distinct radial innate fibrillosity visible under binocular; lamellae moderately broad. Spores 6·5–8·2 × 5·5–7·5μ; basidia 22–30 × 8–9·8μ, 4-spored, some 2-spored; cystidia vesiculose or vesiculose below and with a very broad cylindrical upper portion, the balloon-shaped ones e.g. 36 × 19μ; melleous-hyaline to hyaline, without dark sap; cheilocystidia little differentiated from the pleurocystidia; epicutis of pileus consisting of elongated hyphae with hyaline to pale fuscous dissolved intracellular pigment, the terminal cells most frequently fusoid with gradually, more rarely abruptly, attenuate apex, the latter however mostly rounded, more rarely acute, 100–17–30μ, some subcylindrical and somewhat narrower; hyphae without clamp connexions.

This analysis agrees perfectly with the description of a *Pluteus* reported under this name from Spain by me: among grass near *Abies* 1500 m. alt., Seuva near Plá de Murás, Pireneu Catalán, 27 September 1934, Singer 666 (BA, LE). Here, the *pileus* was squamulose-subgranulose fuliginous-umber, applanate with obtuse low umbo, 50–60 mm. broad. *Lamellae*

pink, crowded, free. *Stipe* pink, smooth, shining, 80 × 7 mm., with somewhat thickened base. *Context* white to pink generally salmoneous pallid to more pink in the stipe, inodorous.

Microscopical characters in agreement with those indicated above for the type.

This is obviously the same species as described by Kühner as *P. carneipes* Kühner, and that called *P. roseipes* by Kühner & Romagnesi.

Pluteus salicinus (Pers. ex Fr.) Kummer (*Agaricus salicinus* Pers. ex Fr.) (Fig. 32)

There is no type of this species as far as I am aware. However, most authors agree now that this is a species with horned metuloids and blueing base, grey pileus and erect, eventually depressed, spinulose squamules in the centre, usually of medium size, the hyphae with clamp connexions. This species is rather common in some parts of Europe and North America but in North America it can easily be confused with *P. brunneidiscus* Murr. and *P. washingtoniensis* Murr. (q.v.) because of the existence of a variety without any tendency to become blue or green in the base of the stipe:

P. salicinus var. **achloes** var.nov.

Pileo griseo, centro spinulose ornato, saepe margine elliptico, radiatim fibrilloso, convexo, depresso circum discum qui est subumbonatus, forma typica minore 19–25 mm. lato. Lamellis roseolis, confertis, latissimis ventricosisque, liberis. Stipite albo, ad cinereum vergente in parte inferiore, mycelio albo ad basin praedito, 26–29 × 2–3·5 mm. Carne alba, inodora. Sporis 6·8–9 × 5·3–6 μ; metuloideis 47·5–69 × 12–17·2 (19·5) μ, ventricosis, ad apicem tantum crasse tunicatis, ad aciem praecipue nonnullis ex integro tenuitunicatis, apice cornutis cornubus tenuibus vel crassiusculis uno, duobus vel tribus, cornubus simplicibus, mediocribus, integris, obliqui svel erectis, pigmento nullo instructis; cheilocystidiis vesiculosis typi *P. cervini* hyalinis, 34–39 × 13·5–16·5 μ; hyphis terminalibus epicutis pilei subulato-subfusoideis, intus fuscidulis, e.g. 105 × 16·5 μ, apice attenuato-effilatis subacutoque gaudentibus; hyphis fibulatis.

Ad lignum emortuum, Michigan (USA), Douglas Lake (Cheboygan Co.), 7 July 1953, Singer N 468 (F).

In view of the existence of such forms as the one described above, I have attempted to find a chemical character that would be useful even in permanently non-discolouring carpophores. Indeed, a mixture of formalin and phenol will generally give a good, constant colour reaction in the base of the stipe of *P. salicinus* even if the discoloration is not very distinct. This colour change appears after a few minutes and produces a vinaceous purple. Phenol alone gives a weak purplish brown reaction in the base. However, the form described here as var. *achloes* does not give these reactions, and we do not consider them as very important because of their failure in this case.

Pluteus semibulbosus (Lasch) Gillet (*Agaricus semibulbosus* Lasch)

Type not available; species understood in the sense of Kühner & Romagn.

Pluteus sororiatus (Karst.) Karst. (*Agaricus sororiatus* Karst.)

The type (part at FH) from Mustiala, Karsten, Fungi Fennici Exsiccati no. 507, 1866, is accompanied by a diagnosis. This collection has spores $8 \times 6{\cdot}5\mu$, with ampullaceous cystidia on both sides and edges of the lamellae, many of them extremely large, epicutis of pileus with many very large pilose terminal cells, as described by me from Caucasian material.

This is the same species as that described by me in *Beih. Bot. Zbl.* II, **48**, 104, 1929, see also *ibid.* **48**, 539, 1931.

It is significant that in these specimens the umbo was smooth or subsmooth, but in one collection became rugose-venose on drying. Except for the smaller spores, *P. luteomarginatus* Rolland seems to be the same thing. However, the difference in spore size is small and not of proven value so that one may assume that *P. luteomarginatus* represents merely younger specimens of *P. sororiatus*. Vacek's description from Czechoslovakia, once on oak and once on spruce, coincides rather well with my own (see *Stud. Bot. Cech.* **9**, 37, 1948).

Pluteus spegazzinianus Sing.

Nothing can be added to the diagnosis of the type collection (LIL, MICH).

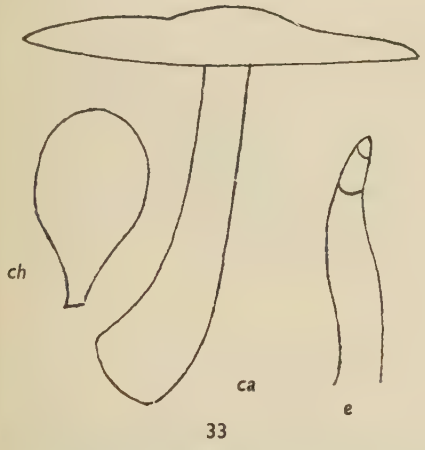
Pluteus spilopus (Berk. & Br.) Sacc. (*Agaricus spilopus* Berk. & Br.) (Fig. 33)

The type from Ceylon (K), and a corresponding picture in the British Museum, show a very deep fuscous pileus with a broad obtuse umbo and radially fibrillose covering, a stipe with black dots reminding one of those of *Gomphidius maculatus*, tapering upward, carpophores of medium size. Specimens (no. 1167) have spores $6{\cdot}5–7{\cdot}7 \times 5{\cdot}7–6{\cdot}3\mu$; hymenium unfortunately collapsed so that the cystidia could not be discerned with certainty, but the cheilocystidia observed were vesiculose and hyaline. Epicutis of pileus consisting of elongate hyphae with fuscous cell sap and rounded tips, about $8{\cdot}8\mu$ thick, some, not necessarily the terminal cells, swollen to 16μ, walls hyaline, some tips of the terminal hyphae with one to two secondary septa and thus doubly appendiculate; all hyphae without clamp connexions.

Similar material collected by Petch (in 1911 and 1917, K) seems to agree very well but is not in very good condition. Some of these carpophores are larger than the type specimens. Among the neotropical species two are extremely close to *P. spilopus*. One was described as *P. fastigiatus* Sing. in Sing. & Digilio (q.v.); the other was described as *P. spilopus* var. *albostipitatus* Dennis (Fig. 34). I believe that the three forms are the elements of a stirps which we may call stirps *Spilopus*; yet all three seem to deserve the status of a species. Dennis's variety should actually be known as *P. albostipitatus* st.nov. ad int. although a slight possibility subsists that *P. compressipes* might, after all, turn out to be identical with *P. albostipitatus* rather than with *P. atriavellaneus* as we prefer to think. To identify it with

the former, one would have to assume that the description of the pileus as 'glabrous' is based on incomplete observation, that the cystidia are as in *P. albostipitatus* rather than in *P. atriavellaneus*, and, most serious, that the giant spores found in both the type and an Argentine collection of *P. albostipitatus*, are absent in some populations. Below, we add a description of the Argentine collection of *P.* ALBOSTIPITATUS:

Pileus fuscous (Chocolate, M. & P., but not reddish), with deeper coloured (African, M. & P.) centre, where it is punctate-spinulose from small dark squarrose particles when dry (not dried), otherwise appearing subglabrous both in fresh and wet and in dried condition (even the squarrulose centre is often hardly visible in this condition), but when fresh and dry more or less



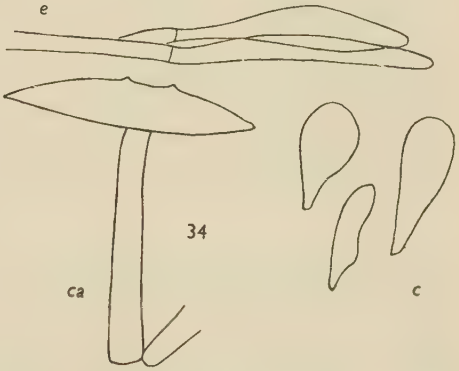


Fig. 33. *Pluteus spilopus*. *ch*, cheilocystidium, × 1000; *ca*, carpophore, × 1; *e*, apex of the terminal cell of epicuticular hyphae, × 1000.

Fig. 34. *Pluteus spilopus* var. *albostipitatus*. *c*, cheilo- and pleurocystidia, × 500; *e*, terminal cells of the epicuticular hyphae of the pileus; *ca*, carpophore, × 2; from the type.

distinctly radially fibrillose with innate fibrils showing little of the white trama, and not becoming rimose, with smooth to short-sulculate margin, not hygrophanous, convex, umbonate, 45 mm. broad. *Lamellae* including edges, pink, soft, rather broad, somewhat ventricose, close, free. *Stipe* white, towards the base mostly pale sordid greyish, subglabrous or subfibrillose, equal, solid, 56 × 5 mm. *Context* white, unchanging, inodorous. *Spores* 6–10 × 4·7–6·7 μ; basidia 24–29·5 × 6·7–9·2 μ; cheilocystidia clavate with broadly rounded apex, hyaline, 32–50 × 8·7–15·3 μ; pleurocystidia similar or ventricose with slight constriction and again ventricose above (not ampullaceous), numerous, hyaline, 59–64 × 17–19 μ; terminal cells of the epicuticular layer everywhere with broadly rounded apex, with evenly dissolved fuscous pigment, ventricose to subfusoid or cylindrical, 46–118 × 12–19 μ; hyphae without clamp connexions.

On dead trunk of a Dicot. tree in subtropical forest, solitary, Argentina, prov. Tucumán, Parque Aconquija, Sierra de San Javier, 17 February 1955, Singer T 2169, LIL.

A specimen of the rather common European *P. plautus* was later misdetermined as *A. spilopus* Berk. & Br., but is quite different. Saccardo renamed the European '*A. spilopus*' non Berk. & Br. *Pluteus podospileus*. This binomial is, therefore, a synonym of *P. plautus*.

Pluteus spinulosus Murr.

Spores 6·5–7·5 × 5·4–5·6 μ; metuloids of the type as described for *P. magnus* (not of the *Cervinus* type), mostly with both apical and lateral, or only with apico-lateral secondary spinules, with comparatively thick and constantly hyaline walls (1–3·3 μ), always acute, near the edge sometimes thinner walled and slightly smaller on an average; epicutis of the pileus consisting of elongated elements, partly, entirely or not at all pigmented (fuscous, intracellular); all hyphae with clamp connexions.

This species was previously restudied from the type from British Honduras (NY) by A. H. Smith, and the analysis given above coincides with his. The fact that the hyphae bear clamps, differentiates this tropical species from the otherwise anatomically similar *P. magnus*, but the latter is in addition much smaller and more strongly pigmented although (as indicated under *P. magnus*) there is a small pigmented (apparently intermediate) form in Florida. This small form is here tentatively treated as *P. australis* Murr.

Pluteus squamosidiscus Murr.

The type from Louisiana (NY) was collected by Earle, No. 55, who calls it small but firm. Spores 7–8·8 × 5·8–7 μ; cystidia not studied because of poor condition of hymenium; epicutis consisting of strictly elongated hyphae which are, in the marginal zone, not particularly voluminous; no clamps seen. According to this somewhat incomplete analysis, this appears to be an independent species of *Pluteus*. There are certainly no horned metuloids.

Pluteus subcervinus (Berk. & Br.) Sacc. (*Agaricus subcervinus* Berk. & Br.) (Fig. 35)

The type from Ceylon (K), no. 917, has a fuscous pileus with appressed fibrils all over, arranged radially and composed of strongly elongated hyphae, the terminal members fusoid to sybcylindric with rounded apex, e. g. 87 × 18 μ; spores 5·8–7·6 × 4·8–5·6 μ; metuloids present, but characteristically scarce, now slightly fuscous inside, with erect horns which are of medium size and simple, solid subobtuse, the walls rather thick; hyphae with clamp connexions.

This seems to be the same as *P. washingtoniensis*, but I hesitate to substitute the epithet *subcervinus* for the American species because of the absence of data on the cheilocystidia and scarcity of the metuloid cells studied, and furthermore the insufficiently described macroscopical characters of the Asiatic species.

Fig. 35. *Pluteus subcervinus*. *c*, carpophores of the type collection, fresh, natural size; *e*, terminal cells of epicuticular hyphae of pileus, × 1000; *m*, metuloid, × 1000.

Pluteus subfibrillosus sp.nov. (Fig. 36)

Pileo porphyriobrunneo vel fuligineo, umbrino, obscure griseo, demum subpallescente usque ad dilute griseum vel dilute fuscum, margine subpallidiore, uniformiter subtiliterque velutino dein fibrilloso, maturitate manifeste fibrilloso-punctato vel fibrillosorimulosulo (carne alba inter fibrillas visibili) in zona marginali, ibidem tunc (maturitate) mediocriter longe striato-sulcato, in juvenilibus subvenoso in centro, conico vel campanulato-truncato, dein expanso et demum applanato subumbonatoque vel umbonato, 30–60 mm. lato. *Lamellis* albis, dein roseis, acie pallidis, demum etiam roseolis, confertis, ventricosis, latis, liberis. *Stipite* albo, dein subtiliter brunneolo-fuscidulo punctulato-fibrilloso et demum fibrillis longitudinalibus umbrinis valde appressis ornato, sed plerumque in duabus tertiis superioribus persistenter albo, indistincte sulculato vel profunde longitudinaliter sulcato, plus minusve incrassato basin versus 30–70 × 6–8 mm. (ad basin), 3·5–4 mm. lato prope apicem. *Carne* alba, carnosa; odore nullo vel haud specifico. *Sporis* 6–7·5 × 5·3–6·2 μ; basidiis 22–30 × 6·5–8·2 μ; cystidiis paucis vel sat numerosis, nonnullis exiguis fusoideisque (46 × 6·5 μ), sed plurimis late ventricosis vel subampullaceis vel ampullaceis, rarius subcapitatis, 34–70 × 12–22 μ, haud incrustatis, apice integris et rotundatis, intus hyalinis vel succo fuscidulo impletis (semper nonnullis fuscidulis praesentibus), pedicellatis; cheilocystidiis numerosis, saccato-vesiculosis (sed ad formam pleurocystidiorum interdum transeuntibus), hyalinis, 38–42 × 15–19·2 μ; epicute pilei ex palisada demum applicato-depressa consistente, ex hyphis elongatis efformata, plerumque pigmento intracellulari fusco dissoluto repletis, membris terminalibus subcystidioideis, subcylindraceis vel ventricoso-subampullaceis vel ventricoso-subellipsoideis, interdum constrictis, constanter late rotundatis ad apicem; hyphis hypodermii etiam partim pigmentatis, cutem formantibus; hyphis omnibus defibulatis.

Ad truncos arborum in America Australi tropicali et subtropicali: Brazil, est. Rio de Janeiro, Angra dos Reis, 30 September 1952, Singer B 433, F. type; est. Rio Grande do

Sul, Taimbesinho, 5 November 1951, Singer B 96, LIL; Argentina, prov. Tucumán, capital, 29 December 1949, Singer T 796, LIL.

Species *P. fibrilloso* Murr., *P. rimosello* Sing. nec non *P. hiatulo* Romagnesi affinis.

Pluteus subgriseibrunneus Murr.

The type from Florida (FLAS) has the same characters as *P. fuliginosus* Murr. and *P. rhoadsii* Murr., and appears to be a synonym of the former.

Pluteus sulcatus Sing. in Sing. & Digilio (Fig. 37)

The type (LIL, MICH) corresponds exactly with the original diagnosis, and is remarkable for its large not much elongated spores (7·5–9 × 6·5–8·2 μ); basidia 25–30 × 8·8–10·2 μ, 4-spored; cystidia most frequently ampullaceous with broad neck, mucronate by a thin and short apiculus, without any fuscidulous pigment, but at times with a slight melleous resinous applicate incrustation, voluminous; cheilocystidia vesiculose, hyaline 21–23 × 12 μ; epicutis of pileus formed by a cutis or depressed trichodermium(?), some terminal members melleous-incrusted, intracellular dissolved pigment in some cells present, melleous or fuscidulous; no clamps; hymenophoral trama inverse. This species is closest to *P. atriavellaneus* Murr. and *P. compressipes* Murr.

Agaricus tephrostictus Berk. & Curt.

The type (K, FH) is in less favourable condition than that of *A. aethalus* published by the same authors from the same region. I agree with Dennis who considers the two as synonyms.

Pluteus tomentosulus (Peck) Peck (*Agaricus tomentosulus* Peck)

Because of an erroneously determined 'authentic' specimen, the species was often misunderstood, and numerous specimens can be found under this name which belong to *P. magnus*. However, the type from New York State (NYS) is not a representative of the *Cervinus* complex. It has no metuloids.

Pileus white, often somewhat pink or pinkish cinnamon at the margin, silky and dry, with finely sericeous and sometimes slightly radially rimose margin, with usually projecting margin, convex, subumbonate or umbonate, 25–78 mm. broad. *Lamellae* white, then pink, with pink edge, rather broad, close, free. *Stipe* white, finely pubescent to tomentose, equal or slightly tapering downward, solid, 50–100 × 5–15 mm. *Context* white, unchanging, inodorous or with a faint agreeable odour. *Spores* 6·5–7·5 × 5·7–6 μ; basidia 25·5–32 × 7·5–8·3 μ, 4-spored; cystidia 48–52 × 15–16·6 μ, hyaline, ampullaceous with tapering neck but obtuse at apex, ventricose in lower, more rarely in middle portion; cheilocystidia like the pleurocystidia but often larger, reaching 69 × 21 μ; epicutis of pileus consisting of repent elongated hyaline hyphae which are cylindrical or slightly fusoid, especially the terminal ones which are often remarkable for a hyaline granular to filamentous content, without pigment, with broadly rounded

apex; terminal cells 35–55 × 7·5–10·5 μ (if cylindrical) or 85–126 × 13·5–16·5 μ (if fusoid); hyphae without clamp connexions.

On dead wood, in Eastern North America west to Michigan, fruiting in summer and fall. *N.Y.*, type. *Mich.*, Douglas Lake, 7 July 1953, Singer N 454 (F).

Pluteus umbrinidiscus Murr.

The type from New York State (NY) has the same macro- and microscopical characters as *P. avellaneus* Murr. although it is somewhat smaller and is slightly lighter coloured in the marginal region than in the centre (which was apparently the reason why Murrill separated it). I consider *P. umbrinidiscus* Murr. as a synonym of *P. avellaneus* Murr.

Pluteus umbrosus (Pers. ex Fr.) Gillet (*Agaricus umbrosus* Pers. ex Fr.) (Fig. 38)

The current interpretation of this species, generally attributed to Ricken, is undoubtedly correct. The description given by Fries, *Systema Mycologicum*, **1**, 200, 1821, has to serve as type, and is characteristic for the species in the sense of Ricken. The spores are 6–6·5 × 4–6 μ; basidia 4-spored; cystidia not of the metuloid type, 49–64 × 16–20 μ, ampullaceous with broad, rounded neck, mostly with dissolved fuscous or brown intracellular pigment, mostly with irregular sterigmatoid excrescences, but thin walled; cheilocystidia 29–54 × 12–22 μ, in shape like the pleurocystidia, but mostly shorter, ventricose to ventricose-mucronate, all with brown cell sap; epicutis of pileus consisting of an interrupted trichodermial palisadic structure which becomes eventually partly depressed, made up by originally erect elements which arise from a cutis of hyaline hyphae (hypodermium), epicuticular elements all hyphous, elongate, with evenly dissolved fuscous intracellular pigment and hyaline wall, the terminal members long-fusoid, with attenuate but broadly rounded apex which is often suddenly thick-walled (2–6 μ), usually entire, 88–300 × 18·5–27 μ; hyphae without clamp connexions. These data were taken from a characteristic collection on elm log, England (K), in order to have the necessary data for a minute comparison with *P. jaffueli* (Speg.) Sing. which replaces *P. umbrosus* in the temperate and subantarctic zone of South America.

Pluteus unakensis Murr. (Fig. 39)

The type from Tennessee (NY) consists of one carpophore on rotten wood. Pileus now whitish, especially on margin, and conspicuously pilose-tomentose; stipe white, sericeous. Spores 4·3–6 × 3·2–4·3 μ; basidia 4-spored, 20–21 × 6·5 μ; cystidia broad and somewhat versiform, hyaline, with broadly rounded apex, 32–33 × 18–20 μ; cheilocystidia similar; epicutis of pileus consisting of irregularly arranged hyphal strands, hyphae often with dense contents but all hyaline, not or very feebly pseudoamyloid, often constricted at the septa, 7·7–23 μ broad, distinctly and constantly elongate, with rounded tips; hyphae without clamp connexions; hymenophoral trama inverse.

A fungus with the same characteristic spores which remind one of *Lepiota*, was collected by me, but the pileus was not tomentose, only with a distinct silky covering, underneath which it was umber, umbonate, 8 mm. broad, with shortly and faintly sulcate margin. Stipe white, smooth and glabrous, 27 × 1·8 mm. (apex 1·2 mm.); context inodorous. Spores 4·5–6 × 3·5–4·3 μ, ellipsoid or broad below and tapering to a rounded apex; cystidia and cheilocystidia near the stipe fusoid-ampullaceous, 30–47 × 9–11·5 μ, hyaline; cheilocystidia near margin of pileus more versiform, usually broadly fusoid or ventricose, or vesiculose, with broadly rounded apex, hyaline, 37–45 × 10·5–12 μ; epicutis with cylindrical to subfusoid hyaline terminal cells of 48–115 × 12–15 μ, with broadly rounded apex, mostly applicate or subascendant; hyphae without clamp connexions. On earth (humus) in frondose woods, 5 miles south of Pleasant View, Emmet Co., Mich., U.S.A., 5 July 1953, Singer N 394 (F). I am convinced that this is conspecific with the type.

Pluteus viscidulus Sing. (Fig. 40)

There is nothing to be added to the original description of the species, but the fact that it occurs in Brazil and perhaps even in Europe (see under *P. pellitus*).

Pluteus washingtoniensis Murr. (Figs. 41, 42)

The type from Washington (Seattle), W. A. Murrill 348 (NY), is in good condition. The stipe is said to have been white but there must have been inconspicuous longitudinal innate fibrils, because some of the hyphae of the surface of the stipe are still filled with fuscous dissolved pigment; the lamellae edge is pink. Spores 6·5–8·8 × 5·5–7 μ; cystidia metuloid with thin, more rarely distinctly thickened, wall (often with only the horizontal apical wall thickened), hyaline, with (2–)4 apical prongs, but these characteristically short and obtuse, sometimes bilobed, rarely with a more elongated prong but this very obtuse or subhorizontal, on sides of the lamellae and also on the edges not numerous; epicutis of pileus consisting of elongated hyphae, the terminal member polymorphous, sometimes cylindrical, sometimes gradually attenuated or mucronate at the apex which, however is always rounded, all with dissolved intracellular fuscous or pale fuscous pigment; all hyphae with clamp connexions.

A similar fungus which I collected in Michigan, has the following characters:

Pileus deep fuscous in the middle, otherwise fuscous, fibrillose, with broadly truncate low umbo, convex-repand, 43–45 mm. broad. *Lamellae* pink, with pink edge, broad, ventricose, 8 mm. broad, close, free. *Stipe* white, with innate, fuliginous fibrils forming longitudinal dark lines, 68–82 × 6–7 mm. *Context* white, unchanging, white in base, inodorous. *Spores* 6·8–7·5 × 4·2–5·7 μ; metuloids partly thick-walled, with oblique short subacute prongs which are short and generally not conspicuous, 58·5–72 × 18·5–20·5 μ; cheilocystidia clavate, 46 × 10·5–18·5 μ; epicutis of elongated hyphae, the terminal hyphae versiform, ventricose-ampullaceous,

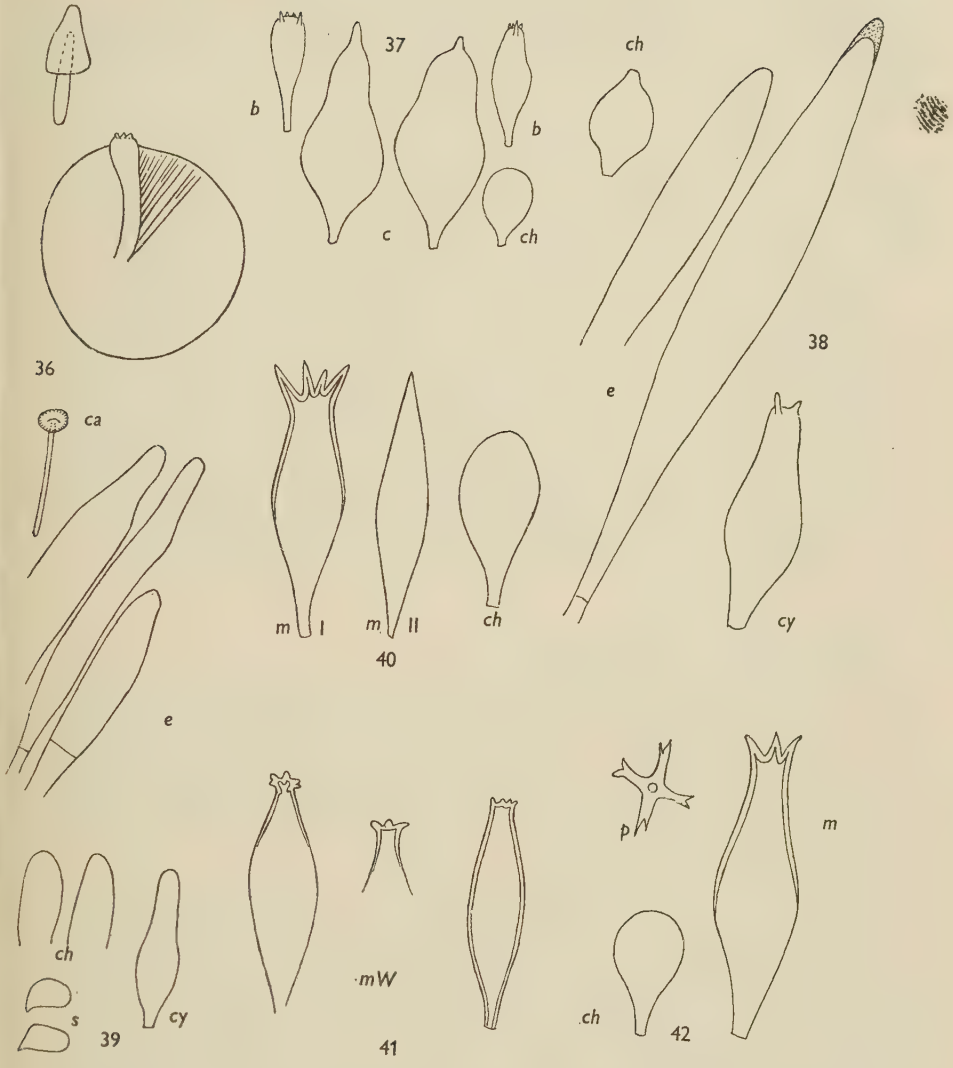


Fig. 36. *Pluteus subfibrillosus*. Young and mature fresh carpophore at one-half natural size.

Fig. 37. *Pluteus sulcatus*. *b*, basidia; *c*, pleurocystidia; *ch*, cheilocystidium. All × 500.

Fig. 38. *Pluteus umbrosus*. *ch*, cheilocystidium; *e*, terminal cells of the epicuticular hyphae of the pileus; *cy* pleurocystidium. All × 500.

Fig. 39. *Pluteus unakensis*. *ca*, carpophore, fresh, one-half natural size; *e*, terminal cells of epicuticular hyphae of pileus, × 500; *ch*, cheilocystidia, × 500; *s*, spores, × 5000; *cy*, pleurocystidium, × 500.

Figs. 40, 41. *Pluteus viscidulus*, *m* I, metuloid of form 1 (*Cervinus*-type), × 500; *m* II, metuloid of form 2 (*Magnus*-type), × 500; *ch*, cheilocystidium, × 500; *Pluteus washingtoniensis*, *mW*, metuloids, × 500, from type.

Fig. 42. *Pluteus* ? *washingtoniensis* (Singer N 81). *m*, metuloid, × 500; *p*, prongs of metuloid as seen from above (axis of metuloid vertical), × 2000; *ch*, cheilocystidium, × 500.

cylindrical, subulate, subclavate, etc., filled evenly with a dissolved fuscous pigment, with rounded tips, 66–9·0 × 6·8–10·5 μ; hyphae of pileus partly with, partly without, clamp connexions, those of the basal mycelium with clamp connexions. On dead trunk, Tahquamenon Falls State Park, Mich., 12 August 1953, Singer N 1263, F.

I believe that this is conspecific with Murrill's species. Unfortunately there seem to be transitional forms between *P. brunneidiscus* and *P. washingtoniensis* Murr. I collected, also in Michigan, a form with very indistinct longitudinal innate fibrils on the stipe, with large (60 mm.) pileus and stipe (60 × 10 mm., apex 5 mm. broad) where the cheilocystidia were vesiculose as in *P. cervinus* and the metuloids more numerous, with conspicuous more or less upright and mostly bifid-forked prongs (3–4 of them, of these 0–4 bifid). This is N 81 from the same station as above, but fruiting early in the year, 19 June 1953, F (Fig. 42). It is also remarkable for the fact that only few hyphae bear clamp connexions while the majority do not. This may well be a slightly clamped form of *P. cervinus* rather than any representative of the *brunneidiscus-washingtoniensis-subcervinus* complex. Finally, there was a third collection, considerably smaller than the others, with condensed pigment in the epicuticular cells which may be a separate species. An older name for *P. washingtoniensis* may be, perhaps, *P. subcervinus* Berk. & Br. as analysed above, from Ceylon.

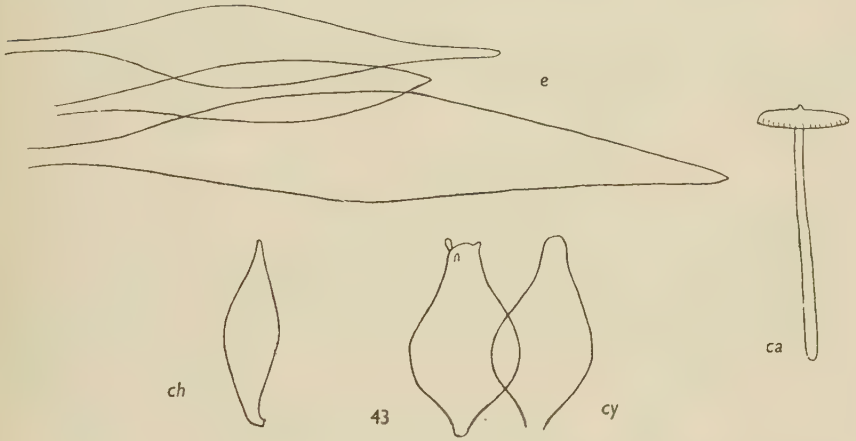
Pluteus whiteae Murr. (Fig. 43)

Spores of the type, collected by Miss White at Bar Harbor, Me., U.S.A. no. 91 (NY), very short ellipsoid to almost subglobose (not globose) 6·5 (7·8) × 4·8–5·5–(6·5) μ; basidia 4-spored 22 × 7·3–7·6 μ; cystidia large but not very conspicuous, at times thinly incrusted by a likewise inconspicuous pale melleous 'wall', but usually hyaline or pale yellowish, smooth, ventricose, 74–79 × 27–32 μ; epicutis of the pileus in poor condition, but apparently not cellular.

This specimen would be nearly worthless were it not accompanied by a coloured picture which shows the fresh specimen with a gold-brown pileus with sulcate margin and brown granules. It is of rather more than medium size. Since the stipe is white, it may well be that this coincides with collections made by me in Virginia. These collections were originally determined as *P. leoninus*, but differ in a number of less significant characters so that it may be possible that the typical European *P. leoninus* does not occur in North America:

Pileus yellow (Golden Rod, M. & P.) with Sudan br. (M. & P.) fibrillosity and the centre entirely 'Sudan br.', in addition, subgranulose, with finely and shortly transparently striate margin, convex-repand, with a small but distinct umbo, 22 mm. broad. *Lamellae* pink, ventricose, broad, free. *Stipe* entirely white, finely longitudinally striate, 63 × 3·5 mm. and very slightly tapering to apex. *Context* white, inodorous. *Spores* 6–6·8 × 5–5·3 μ; cystidia 40–75 × 15·5–30 μ, hyaline to palest fuscidulous-hyaline, ampullaceous, with short excrescences at apex, more rarely entire, with 7·8–11·5 (15·5) μ broad neck; cheilocystidia 40–68 × 11·3–23 μ, with a very thin mucro (10 μ long) at the apex; epicutis of pileus with pale fuscous

(not yellow) to hyaline fusoid cell with effilate-subobtuse to subacute terminal cells 70–230 × 14–32 μ; hyphae without clamp connexions. On rotten wood, 30 June, 1947, Mt. Lake, Giles Co., Va., U.S.A., Singer V 366, F.



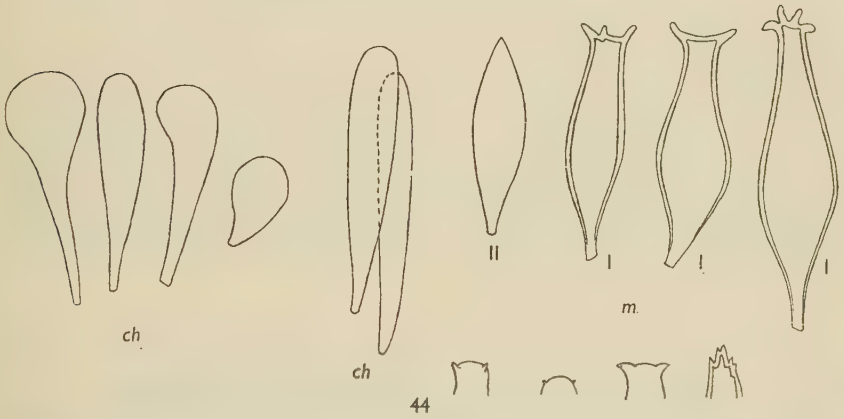


Fig. 43. *Pluteus whiteae* (Singer V 366). *e*, terminal cells of epicuticular hyphae of pileus, × 500; *ca*, fresh carpophore, one-half natural size; *ch*, cheilocystidium, × 500; *cy*, pleurocystidia, × 500.

Fig. 44. *Pluteus xylophilus*. *ch*, cheilocystidia; *m*, metuloids (I, of form 1, i.e. *Cervinus*-type; II, of form 2, i.e. *Magnus*-type); below apices of other metuloids of both type I (from zone of edges of lamellae) and type II. All × 500.

The white stipe, absence of rugosity on pileus, and shape of the cheilocystidia distinguishes this from *P. flavofuligineus*, smaller spores and white stipe from *P. sororiatus*. It is possible that all these forms are merely geographical and local races of a very variable *P. leoninus*, but for the time being, and for the present purpose, I think it better to keep them separate.

Pluteus xylophilus (Speg.) Singer (*Entoloma xylophilum* Speg.) (Figs. 44 and 4)

The type from La Plata (LPS) is a *Pluteus*. It was transferred on the basis of a preliminary examination of the type collection (h.n. 22992) but later re-examination shows that this collection consists of fragments of a carpophore mixed with a single fragment of another fungus in which the cuticular layer is better preserved than in the others. Not being aware of this mixture, I indicated (*Lilloa*, **23**, 203, 1950) erroneously the cuticular characters of the foreign fragment. However, the species as described (that is, the remaining fragments), has a hyphous epicutis, consisting of repent thick to thin, more frequently thin, elongated hyphae with hyaline, melleous or fuscidulous cell sap. The other data are correct except that a thorough search of the hymenial layer shows that apart from the obtuse or poorly pronged metuloids, there are also some with acute apex, and even with side spinules near the edge, and further away from the edge region, numerous metuloids with normal obtuse or acute prongs are found which are not much different from those of *P. cervinus*; cheilocystidia dimorphic, some clavate-elongate, others (fewer) broadly vesiculose as in *P. cervinus*; hyphae without clamp connexions. The pileus is described as cream and pink but the pink colour must have come from spore dust. The colour exactly matches the paler forms of *P. cervinus* var. *brasiliensis*, not reminiscent of one of the white species. The stipe is described as white, but some of the superficial hyphae of the lower portion of the stipe are still filled with a fuscidulous sap, and we therefore conclude that the stipe was innately longitudinally striped by dark fibrils, as usually found in the above cited variety, at least in the paler specimens. Consequently, *Entoloma xylophilum* Speg. is a synonym of *P. cervinus* var. *brasiliensis* Bres., or, if one prefers to give that variety specific rank, the latter becomes a synonym of *Pluteus xylophilus* (Speg.) Sing.

2. Section *Celluloderma* Fayod (1889)

Pluteus admirabilis (Peck) Peck (*Agaricus admirabilis* Peck)

The type from Greig, N.Y. (NYS), consisting of numerous specimens collected by Peck between July and September 1870, is accompanied by a coloured picture showing the specimens with rugose centre, striate pileus, and a golden yellow colour, narrowly hollow stipe with white basal tomentum; pileus umbonate. Its microscopical characters agree perfectly with the current interpretation of this species in North America. I have numerous personal collections, all with the essential anatomical characters of the type, but in view of the common occurrence of this species, it is not redescribed here. We would merely mention that the pileus is usually Aureolin Y. (M. & P.), deeper in the centre and a clearer golden-melleous on margin when wet. Both cheilocystidia and cystidia are vesiculose to balloon-shaped, e. g. $30 \times 18\mu$.

However, the correct name of this species is *Pluteus chrysophlebius* (Berk. & Rav.) Sacc. (q.v.) which has priority.

Pluteus alachuanus Murr.

The type from Magnesia Springs, Alachua Co., Fla. (FLAS) is in good condition. Spores 5·8–6·8 × 4–6 μ; cystidia 45–47 × 8·5–15 μ, hyaline, vesiculose or broadly fusoid; epicutis of pileus with cells 20–46 μ in diameter filled with fuscous cell sap.

These data, combined with the macroscopical characters (see *Fla. Acad.* 7, 118, 1944 (1945)), prove that *P. alachuanus* Murr. is a synonym of *P. jamaicensis* Murr.

Pluteus albolineatus Berk. & Br. (Fig. 45)

The type from Ceylon (K) is represented by specimens, and also by a drawing and specimens at the British Museum. Spores 5·8–6·5 × 5·2–5·8 μ, very short ellipsoid to subglobose; cystidia broadly cylindrical to vesiculose, hyaline, obtuse; epicutis distinctly cellular. Pileus almost blackish, but rimose (white lines showing where the cuticle is fibrillosely split); stipe not white; umbo present.

This species is evidently closely related to *P. rimosus* Murr., *P. tucumanus* Sing., and *P. grandineus* (Berk. & Br.) Sacc.

Pluteus alborugosus Kühner & Romagnesi, see *P. hololeucus* Sing.

Pluteus aurantiacus Murr.

The type from New York State (NY) has spores 6·3–7·3 × 5·5–6 μ; cystidia on sides and edge of lamellae numerous, yellow on edge and 13–17 μ broad; epicutis cellular, cells hyaline to yellowish. Pileus visibly striate, and rugose in centre, glabrous, edge of lamellae not discoloured.

This is obviously a synonym of *P. aurantiorugosus* (Trog) Sacc.

Pluteus aurantiorugosus (Trog) Sacc. (*Agaricus aurantiorugosus* Trog)

The type from Switzerland (P) has short ellipsoid spores and still recognizable obpiriform cells forming the epicutis. This is the same as the preceding species and *P. caloceps* Atk. It has clear priority over both. *P. coccineus* Mass. is apparently also the same.

Pluteus brunneopictus (Berk. & Br.) Sacc. (*Agaricus brunneopictus* Berk. & Br.) (Fig. 46)

There is a picture at the British Museum, and specimens at Kew and the British Museum. The picture shows this with white stipe, deep fuscous and radially fibrous pileus, subumbonate. Spores 5·3–5·8–7·3 × 4·5–4·8 μ, not globose and some rather strongly elongate; cheilocystidia slightly umbrinous from a dilute intracellular pigment, at least some of them vesiculose; epicutis cellular, with internal pigment bodies (bright chestnut-umber).

Nolanea bruchii Speg. (Fig. 47)

Spores 5·8–6·8 × 4·7–6·2 μ; cheilocystidia few preserved, vesiculose cystidia collapsed; epicutis of pileus probably a continuous epithelium (although in radial sections not now very evident), yellow, certainly very reduced by the manner of preparation and frequently showing elongate hyphae in the uppermost layer, mostly destroyed by moulds; no clamp connexions seen. The specimen is accompanied by an outline drawing, showing convex non-umbonate pileus and equal stipe; the pileus is smooth in the centre; there is whitish basal tomentum. The substratum is still joined with the carpophore: a piece of dead wood.

The type from Cordoba (Alta Gracia, coll. Bruch 225) had been studied by me before (*Lilloa*, **23**, 203, 1950), and the species was then transferred to *Pluteus*. A more detailed study of the specimen for the purpose of the present paper showed that the apparently hyphous epicutis seems to be a strongly reduced cellular layer. It would then be identical with the fungus described by Singer & Digilio as *P. admirabilis* from Argentina, differing from that species (recte *P. chrysophlebius*) in smooth or scarcely venose pileus (only rarely very slightly rugulose when drying), and perhaps slightly smaller average size. This is hardly more than a poorly differentiated geographical race of the North American type. We shall call it **P. chrysophlebius** ssp. **bruchii** (Speg.) comb. nov. (*Nolanea bruchii* Speg., *Bol. Acad. Nac. Cienc. Cordoba*, **29**, 124, 1926) for the purposes of this paper.

Pluteus caloceps Atk.

The type, from Michigan (CU), and paratype, from New York State (CU), are in good condition and identical with each other. They have the following microscopical characters in common; spores 5·3–8·7 × 4·3–5 μ; many definitely cylindrical, some even with suprahilar depression, rarely subglobose (the smaller ones); basidia 22·5–28·5 × 6·3–7·2 μ, 4-spored; cystidia ventricose, cheilocystidia often vesiculose but variable, not well preserved; epicutis of pileus consisting of a hymeniform layer of hyaline to pale yellow or light golden yellow globose to obpiriform or ventricose-vesiculose and pedicellate cells which vary between 21–43 × 15·5–43 μ, and may be isodiametric or as elongate as 40 × 17·2 μ; hypodermium a cutis of hyphae carrying pale golden yellow to yellow intracellular pigment; hyphae without clamp connexions.

This is a synonym of *P. aurantiorugosus* (Trog) Sacc.

Pluteus chrysophlebius (Berk. & Rav.) Sacc. (*Agaricus chrysophlebius* Berk. & Rav.)

The type from South Carolina on rotten *Carya* stumps, coll. Ravenel, det. Berkeley (FH) has spores 6–7 × 5·5–6·5 μ, subglobose; basidia 19·5 × 6–7 μ, 4-spored; cystidia collapsed, not very numerous; epicutis of pileus consisting of hyaline spherocysts.

This is the oldest name available for the species usually called *P. admirabilis* (Peck) Peck in North America.

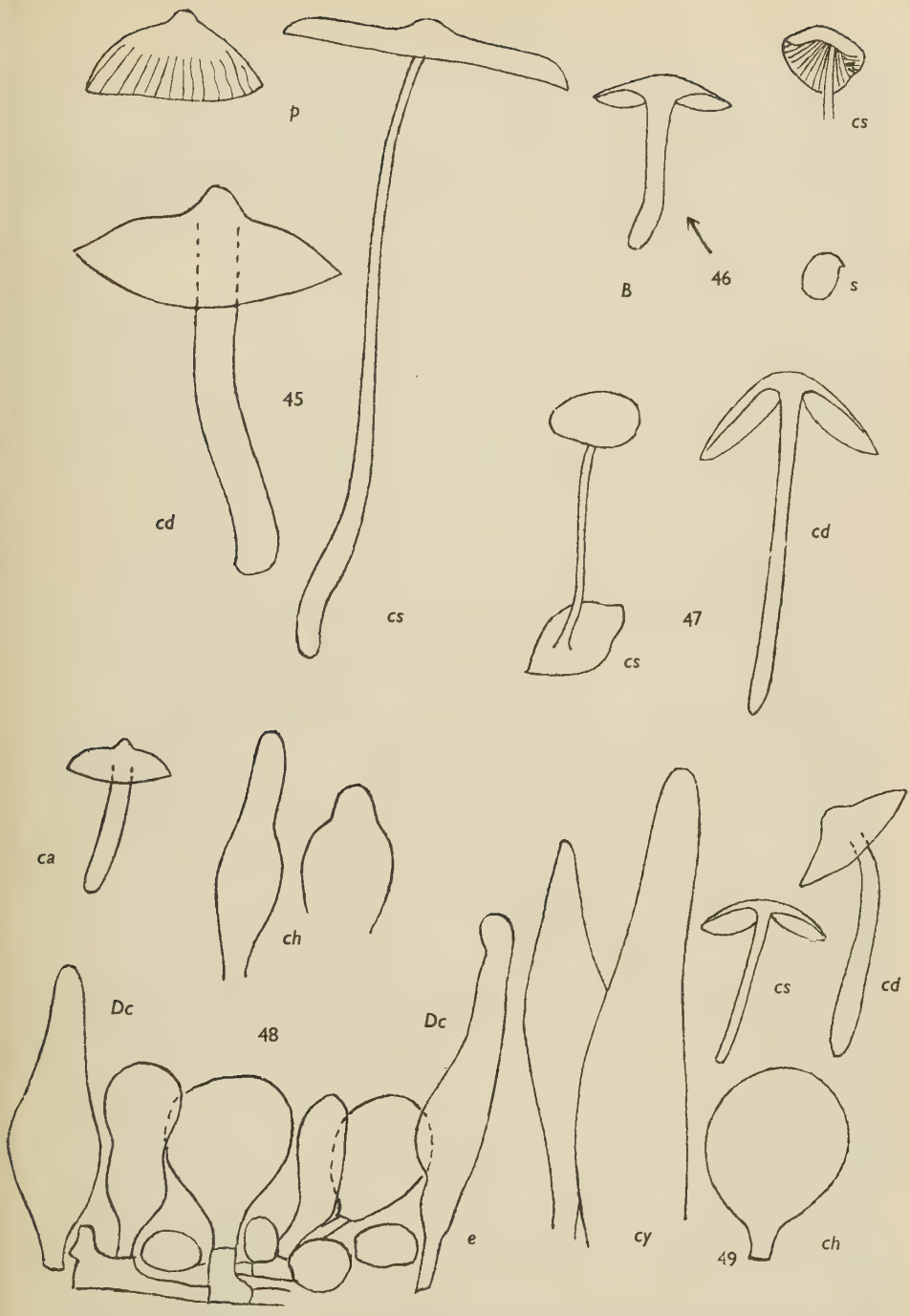


Fig. 45. *Pluteus albolineatus*. *p*, pileus from dried material at Kew; *cs*, dried carpophore, type; *cd*, fresh carpophore from drawing of Broome collection at the British Museum. All × 1.

Figs. 46, 47. *Pluteus brunneopictus*. *B*, section of fresh carpophore; *Pluteus chrysophlebius* subsp. *bruchii*; *cs*, carpophore as preserved at Spegazzini Institute; *cd*, carpophore in longitudinal section, del. Spegazzini, all × 1; *s*, spore, × 1000.

Fig. 48. *Pluteus eugraptus*. *ca*, carpophore, fresh, from type collection, × 1; *ch*, cheilocystidia, × 1000; *e*, structure of the epicutis (*Dc*, dermatocystidia of pileus), × 1000.

Fig. 49. *Pluteus fusconigricans*. *cs*, carpophore from dried type material at Kew, × 1; *cd*, carpophore from original drawing from fresh type material, × 1; *cy*, pleurocystidia, × 1000; *ch*, cheilocystidium, × 1000.

Pluteus cinereofuscus Lange

I have collected material exactly corresponding to the description and picture; I think that no type exists. This species differs from other forms of the *Nanus*-complex in size, pileus surface and colour. My material came from the Caucasus (W). See also *P. thomsonii* Berk. & Br.

Pluteus coccineus Mass.

I have not seen or studied the type, but material determined so by Pearson from Bookham, England, on stump of *Fraxinus*, is identical with *P. aurantiorugosus* (Trog) Sacc. Its spores are 5·5–7·3 × 4·5–5·5 μ; epicutis of pileus composed of a hymeniform layer of obpiriform to clavate-vesiculose short cells, these thick-walled above, light lemon yellow inside, e. g. 31 × 15 μ; hyphae without clamp connexions.

Pluteus eugraptus (Berk. & Br.) Sacc. (*Agaricus eugraptus* Berk. & Br.) (Fig. 48)

The type from Ceylon is represented in the British Museum by a coloured sketch and specimens, at Kew by specimens. The latter have ellipsoid spores, 5·8–7·3 × 4·5–5·3 μ; basidia 33 × 8·2 μ, 4-spored; deep brown vesiculose-ampullaceous to ampullaceous cheilocystidia which make the gill edge black; epicutis of the pileus consisting of a palisade of heterogeneous bodies, mainly of two types, (1) obpiriform to (rarely) cylindrical short walls corresponding to the ordinary epicuticular elements of this section, and (2) erect or ascendant dermatocystidia-like elongate bodies, ampullaceous to ampullaceous-subcapitate and pedicellate, the former about 27 μ long, the latter 40–58 × 8–14 μ, all rising from the almost subisodiametric small cells of a subhymenium-like hypodermium; all these elements filled with a gelatinous-condensed fuscous intracellular pigment. Since in certain stretches of the surface of the pileus the short elements are present almost exclusively, the pileus appears slightly uneven under binocular but does not seem to be rugose or sulcate; it is umbonate, small, with small cylindrical stipe which is brown inside and out, more so at the base. This is a typical representative of an interesting group of species intermediate between the two main sections in so far as both elongate and vesiculose-obpiriform epicuticular elements are present. Of the species entering this group, *P. eugraptus* (Berk. & Br.) Sacc. is the only one with black gill edge.

A species obviously identical with this Asiatic *Pluteus* was collected in Argentina:

Pileus very deep brown, velutinous, eventually becoming very densely fuliginous-fuzzy with the white context visible only under a lens, slightly sulcate or smooth, eventually sulcate, often not quite circular, convex, eventually flattened, with or without a small, low umbo, 15–17 mm. broad. *Lamellae* sordid pink, with fuliginous edge, broad and ventricose, close, free. *Stipe* with fibrils concolorous with those of the pileus all over from apex to base, but at apex more scattered than otherwise, below the sordid-

pallid trama of the stipe visible, equal or subequal, sometimes curved, 12–20 × 1·2 mm. *Context* white to sordid pallid, unchanging, inodorous. *Spores* short-ellipsoid to subglobose, 4·8–6·2 × 4–5 μ; basidia 22·5–24 × 6–7·3 μ; cystidia fuscous, very few hyaline, ventricose and mostly ampullaceous, smooth, 22·5–43 × 10–14·7 μ; cheilocystidia forming a broad border on the edge of the lamellae (which is heteromorphous), very similar to the elements of the epicutis but not subglobose, the smaller ones often broadly ventricose or subclavate, e. g. 20–22·5 × 7–10 μ, the larger ones with attenuated narrow tip or with broadly rounded tip, ventricose or sometimes ampullaceous, up to 130 μ long, and 10–35 μ broad, filled with an evenly dissolved or gelatinously condensed fuscous pigment; hymenophoral trama hyaline, or with some few brownish hyphae intermixed, inverse; epicuticular elements of two types, (1) spherocysts or short obpiriform cells, 24–40 × 21·3–30·5 μ, (2) dermatocystidia, either relatively broad and broadly rounded, or relatively narrow and attenuate to a subacute apex, in age often ampullaceous (with a 'neck') elements observed, all with thin walls and gelatinously condensed intracellular fuscous pigment, 62–140 × 12·7–44 μ; all hyphae without clamp connexions.

On old fallen dicotyledonous tree in subtropical forest, solitary, Argentina prov. Tucumán, Yerba Buena, 12 February 1955, R. Singer, T 2153, (LIL).

Pluteus fulvibadius Murr.

The type from Glen Brook, Ore., U.S.A. (NY) was collected by Murrill (no. 760). Spores 6–6·8 × 5·5–6 μ; basidia 26–35 × 7–7·7 μ, 4-spored; cystidia 40–66 × 12–23 μ, ventricose with narrowed but broad 'neck' and broadly rounded at the apex, not numerous; cheilocystidia numerous, much like the pleurocystidia, saccate-vesiculose, shorter than the pleurocystidia; hymenophoral trama inverse; epicutis of pileus cellular, cells with round brown pigment-bodies, almost chestnut-brown; basal tomentum consisting of smooth, thin-filamentous, hyaline or subhyaline, always thin-walled hyphae without clamp connexions. There is just one carpophore which is rather large and with chestnut coloured pileus, apparently rugose, with strongly elongated stout stipe, distinctly humigenous. This is apparently a good species.

Pluteus fusconigricans (Berk. & Br.) Sacc. (*Agaricus fusconigricans* Berk. & Br.) (Fig. 49)

There are pictures and specimens at the British Museum, and good specimens at Kew. This is a dark-edged species. Spores 6·5–9 × 5·2–7·3 μ; cystidia fusoid to fusoid-ampullaceous, with brown intracellular pigment either in the middle zone only, or else in the basal third or half, the rest being hyaline, seem to be indistinctly incrusted by a rigid matter forming a belt so that they are likely to break above and below it, scattered far away from edge, numerous near edge, and crowded at edge, sometimes mixed with a few occasional vesiculose short cheilocystidia; epicutis cellular, with condensed pigment bodies inside (dark fuscous). This grew on wood. It is the only Ceylon species with this homogeneous cellular epicutis structure and black gill edge. The stipe is illustrated as pink.

Pluteus globiger Sing. in Sing. & Digilio

I have nothing to add to the original diagnosis, covering the type and additional collections from Argentina. This is different from the closely related *P. chrysophaeus* of the northern hemisphere in having almost geometrically globose spores, and a few other small characters of its own.

Pluteus grandineus (Berk. & Br.) Sacc. (*Agaricus grandineus* Berk. & Br.) (Fig. 50)

The type from Ceylon, no. 919, collected 18 December 1868 (K) has spores 7·3–9 × 5·8–6·7 μ; hymenium collapsed and cystidia not seen; epicutis above a hypodermium forming a cutis, the epicutis forming a

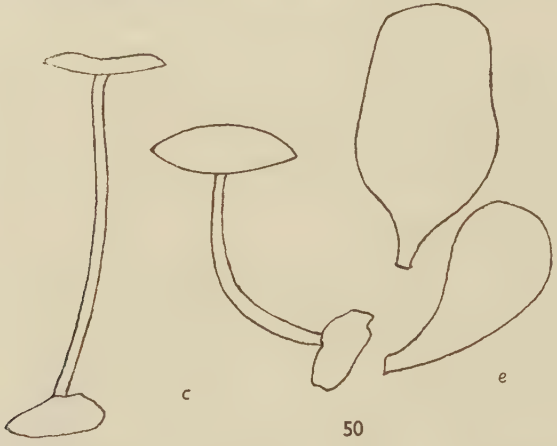


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Fig. 50. *Pluteus grandineus*. *c*, carpophores from type, × 1; *e*, cells of the epicutis of the pileus, × 1000.

subhymeniform layer of short elements, either vesiculose-clavate or vesiculatose-ampullaceous, with pigment condensations inside or filled completely by a fuscous pigment. Pileus apparently very finely rivulose-verruculose in the centre and sulculate on the margin. However, the verruculose aspect, which gave the species its name, appears, upon microscopical examination, to be caused by spore accumulations. No pictures accompany the material. This may be close to *P. rimulosus* Romagnesi.

Pluteus hololeucus sp.nov.

Pileo candido, reticulato, 11–28 mm. lato; lamellis roseis, latis; stipite candido, pruinato; carne alba immutabili, inodora; sporis globosis vel subglobosis, 5·3–7 × 5·3–6 μ; basidiis 4-sporis; cheilocystidiis ventricosis vel ventricoso-ampullaceis; cystidiis hyalinis, tenuitunicatis, ampullaceis, rarius ventricoso-ampullaceis vel ventricosis, 33–52 × 12–19 μ; hyphis defibulatis; epicute pilei ex epithelio hyalino consistente. Ad truncum emortuum dicotyledoneum in silva subtropicali, Argentina, T 2105 (LIL), typus.

Pileus pure white, glabrous, but micaceous in dry condition, strongly reticulate from raised subradiating lines all over, more rarely only in the

centre, or only distinctly rugulose, with more or less sulculate margin when mature, dry, convex, eventually applanate, often somewhat umbonate, 11–28 (33) mm. broad. *Lamellae* white, then pink (including the edges), broad (4·5 mm.), ventricose, close, free. *Stipe* pure white, very faintly lineate but very distinctly mealy-pruinate, equal, 12–31 × 1·5–3·5 (5) mm.; basal mycelium white; some carpophores somewhat eccentric. Context white, unchanging, inodorous. *Spores* 5·3–7 × 5·3–6 μ, some almost geometrically globose, others more elongate, smooth, stramineous; basidia 4-spored, 20–23 × 7–7·3 μ; cheilocystidia ventricose to ventricose-subampullaceous, hyaline, entire, very numerous, 40–50 × 12–15 μ; pleurocystidia numerous, ampullaceous, fewer ventricose-ampullaceous or ventricose, hyaline, smooth, naked, entire, thin-walled, 33–53 × 12–19·5 μ; hyphae of the inverse hymenophore hyaline, without clamp connexions; epicutis of the pileus consisting of an epithelium of short elements which are globose to short-clavate-vesiculose, 42–47 × 18–38 μ, smooth, hyaline, basal septum not clamped.

On dicotyledonous trunk in subtropical forest at 1000 m. alt., gregarious, Argentina, prov. Tucumán, Ciudad Universitaria, Sierra de San Javier, 31 January 1955, R. Singer T 2105 (LIL).

This is extremely close to *P. alborugosus* Kühner in Kühner & Romagnesi which, in turn, is merely a new name for the rare European species described and figured by Lange as *P. semibulbosus*. Since nothing, except the description and illustration (Lange, pl. 71, C), is known, we can compare our species only with Lange's data. The latter differs only microscopically, having much longer cystidia and relatively more elongated spores. If *P. hololeucus* were a European species, I would be inclined to consider it as a subspecies or variety of *P. alborugosus*. See also *P. roseocandidus*.

Pluteus iguazuensis sp.nov. (Fig. 51)

Pileo atrofusco, sulcato, haud rimoso, 20 mm. lato. Lamellis ventricosis. Stipite candido, base pileo concolore, apice baseque incrassato, 22 × 1·5 mm. Sporis 5·8–6·2 × 5–5·5 μ, subglobosis; cystidiis subvesiculosis, hyalinis; epicute pilei cellulari, cellulis globosis pigmento dissoluto impletis. Ad lignum putridum, Iguazú, Misiones, Argentina, 26 Novembri 1949, Singer & Digilio (LIL). Est *Pluteus aethalus* sensu Sing. & Digilio (non Berk. & Curt.), *Lilloa* **25**, 271, 1952.

Fig. 51. *Pluteus iguazuensis*. *e*, epicuticular cell; *ch*, cheilocystidium; both × 500.

Pluteus jamaicensis Murr.

The type was collected by Earle in Castleton Gardens (NY). Spores 5·5–6·5 × 5–5·5 μ, subglobose (not geometrically globose); cheilocystidia ampullaceous to subampullaceous-vesiculose, hyaline, 24–30 × 8·7–13 μ;

epicutis cellular, cells with completely dissolved intracellular pigment. The pileus is rugose in the centre and very slightly rimose outwards; the margin is somewhat sulcate in some specimens although the description calls it smooth. The stipe seems to have been white; there is a basal tomentum which is white.

This species was described by Singer & Digilio (*Lilloa*, **25**, 268, 1950) as '*Pluteus phlebophorus* (Ditm. ex Fr.) Gillet *var.*?'.

Pluteus keissleri Sing.

The type from the Caucasus (W) is very characteristic, and different from other European and Asiatic species.

Pluteus laetifrons (Berk. & Curt.) Sacc. (*Agaricus laetifrons* Berk. & Curt.)

The type from Cuba is Wright 94 (FH, K). It has spores varying between globose and almost globose, 4·5–5·5 × 4·3–5·3 μ; basidia 19·5–5·5 μ, 4-spored; cystidia rather broad, rather scattered and now mostly collapsed; epicutis greatly deteriorated by moulds, but spherocysts still visible, globose to subglobose, hyaline. Carpophores small with orange red pileus, on rotten wood.

Pileus when fresh Scarlet to Brazil Red with Grenadine Red (M. & P.) margin, or English Red, Grenadine Red, with Morocco Red (R.) umbo, the marginal zone usually minutely cracked and then a pallid to Light Cadmium (M. & P.) layer showing between the broken cuticle with almost indistinctly (very shortly and slightly) striate margin, later almost striped yellow on more orange ground, subconical, then convex and repand, subumbonate to umbonate, 10–15 mm. broad. *Lamellae* sordid yellowish, eventually more pinkish, up to 2·5 mm. broad, ventricose, close to subdistant, free. *Stipe* Pinard Yellow (R.) with Cadmium Yellow minute floccons, equal or more often slightly tapering upward, hollow when mature, 12–19 × 1–2 mm. *Context* pallid or orange yellow in pileus, pallid or pale yellowish in the stipe; inodorous. *Spores* 4·5–6·8 (7·5) × 4·3–6 μ, varying from subglobose to geometrically globose, always a large number of globose spores present in spore prints; basidia 19·5–33·5 × 5·5–10·8 μ, i.e., sometimes remarkably voluminous in relation to spore size, 4-spored; cystidia vesiculose-submucronate, e. g. 33–41 × 16–24 μ; cheilocystidia similar or more vesiculose, all cystidial elements hyaline; epicutis of pileus consisting of obpiriform to globose cells which are hyaline, thin-walled, 16–39 μ diam.; no clamp connexions seen. On wood, fallen to the ground and rotten, more rarely on humus, fruiting from September until April; Florida, Dade Co., Matheson Hammock, 3–4 October 1942, Singer F 933, 933a (F); *Trinidad*, near Arima, 25 September 1949, Dennis no. 67 (K); *Cuba* (type).

Agaricus leoninus var. *chrysophaeus* Pers. ex Fr., see *Pluteus phlebophorus.*

Pluteus longistriatus (Peck) Sacc. (*Agaricus longistriatus* Peck) (Figs. 52, 53)

The type from New York State (NYS) was collected by Peck in July on decaying wood. This is a well-known *Pluteus* in North America although it is often confused with *P. atriavellaneus* Murr. which may assume a similar appearance. The type has spores 7–7·8 × 5·5–6·7 μ and a 'mixed epicutis', i.e., with elongated or cystidioid bodies projecting beyond a cellular hymeniform base:

Pileus varying from Mouse Grey or Cinnamon Grey to deep sepia-fuliginous, sometimes darker in centre, sometimes paler in centre, with

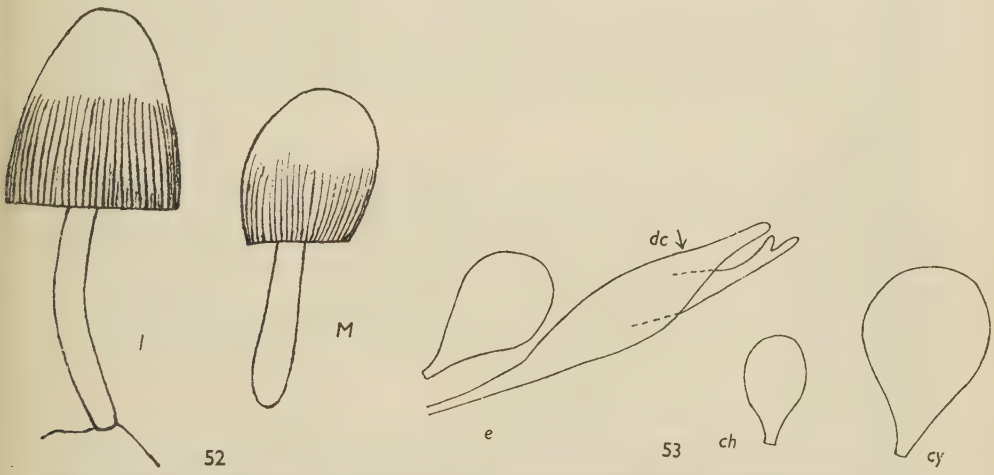

Fig. 52. *Pluteus longistriatus.* Carpophores, × 1; *M*, from Michigan, *I*, from Illinois.

Fig. 53. *Pluteus longistriatus. e*, elements of the epicutis of the pileus (*dc*, dermatocystidium of the pileus); *ch*, cheilocystidium; *cy*, pleurocystidium. All × 500.

rather loosely attached granules or floccons especially in the centre, but often appearing completely naked and glabrous, often with slightly rivulose rimulose surface and rugulose centre, the margin always deeply sulcate and in mature specimens sulcate-plicate over at least one half of the radius, ovoid to campanulate, 12–30 mm. broad, 12–19 mm. high, often slightly umbilicate in the centre. *Lamellae* white with white edge, then pink, at first ascendant, broad or rather broad, eventually ventricose, in young caps often concolorous with pileus in the upper zone in the marginal region, later always unicolorous, close, free. *Stipe* white, usually longitudinally striate, and sometimes fuliginous-fibrillose-punctate at the base which tends to be slightly thickened, glabrous above, 30–70 × 1·5–5 mm. *Context* white or greyish white at first with slightly more cinereous shades in base and near margin in young specimens, later usually all white, or pallid, relatively not very thin, moderately fragile, unchanging, inodorous

or with a slightly acid-fungine odour. *Spores* 4·8–8 × 4·4–6·7 (mostly 6·8–7·8 × 5–5·7) μ; cystidia vesiculose to ventricose and then often with a short and thin to thick mucro, 49–57 × 10–15 μ if ventricose, and up to 36 μ broad if vesiculose, the mucro of the ventricose cystidia usually thin and sometimes subcapitate, all cystidia occasionally with an inconspicuous applicate resinous pale melleous incrustation which makes them very pale melleous, others completely hyaline, without any intracellular pigment; cheilocystidia very similar to the pleurocystidia (both types) but often smaller; epicutis of the pileus consisting of two very different types of elements: (1) balloon-shaped or obpiriform-vesiculose cells, corresponding to the cells of the *Nanus*-group, 44–45 × 21–24 μ, (2) cystidioid elongated, originally erect to ascendant terminal hyphae which are ventricose either below or in the middle, tapering conically or with a thin neck toward a subacute or obtuse thin tip, 43–170 × 14–18 μ, or sometimes narrower, rarely broader, as well as (3) often elongated, transitional cells with rounded apex present, e. g. cylindrical, 57–15 μ, all these elements with either completely dissolved fuscidulous cell sap or (in the Florida collection) with partially condensed brown internal pigment, occasionally with slight yellowish incrustations, often partly hyaline; all hyphae without clamp connexions.

On rotting wood of *Acer*, *Pyrus*, *Quercus*, etc., Eastern United States and west at least to Illinois: *N.Y.*, type; *Fla.*, Dade Co., Matheson Hammock, Singer F 893 (F); *Mich.*, Cheboygan Co., Wolf's Bog, 26 June 1953, Singer N 174 (F); *Ill.*, Geneseo, June 1913 with photo, E. T. and S. A. Harper 3553 (F) (probably).

The Florida collection was less sulcate and had pigment condensations in the cuticle.

Pluteus luctuosus Boud. (Fig. 54)

The type of this species is probably in the Boudier Herbarium (PC), but the interpretation of the species does not cause any difficulties. *P. luctuosus* is widely distributed since it has also been found in Argentina (see redescription in *Lilloa*, **25**, 270, 1950).

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Fig. 54. *Pluteus luctuosus*. Fresh carpophore from collection T 1234, × 1.

Pluteus ludovicianus Murr.

The type from near New Orleans, La. (NY) was collected by Earle, no. 130. This is a comparatively large species of the *Nanus*-complex with

spores 6–6·8 × 4·5–6 μ; basidia 20 × 8·8 μ, 4-spored; cystidia numerous on sides and edges, somehow vesiculose but now many collapsed, hyaline, relatively large; epicutis definitely cellular.

I have no experience with fresh material of this species. It is larger than most species of its group, but differs from the large European form (*P. thompsonii*) in colour and spore measurements. It seems to be very close to *P. phlebophorus*.

Pluteus lutescens (Fr.) Bres., see *Agaricus nanus* var. *lutescens*.

Pluteus melleipes Murr.

The type from New York State (NY) was collected by Earle no. 1589. Spores 6–7 × 4·8–6 μ; cystidia more or less vesiculose, hyaline, e. g. 29 × 13–19 μ; epicutis of pileus consisting of vesiculose cells which are either hyaline or filled with a very pale homogeneous fuscidulous cell sap. Earle 1629, under the same name, seems to represent the same species. This may be too close to *P. chrysophaeus*, sensu Konrad & Maublanc.

Pluteus minutus Pat.

The type from the Botanical Garden of Hanoï, Tonkin (Indo-China) is preserved (FH). It is an extremely small *Pluteus* which was originally characterized by its collector (Demange, no. 217) as having pulverulent-pruinose pileus which was said to have been 'bistre-roux', with 'fauve' stipe. The measurements are somewhat puzzling. Demange indicated them as 0·005 (m.?) for both pileus diameter and length of stipe. Patouillard changed this to 3–6 mm. for the pileus and 5–8 mm. for the stipe. Yet the preserved specimens are now smaller than these dimensions. Pileus 1·5–2 mm. broad; stipe 3–3·5 mm. long. Patouillard described the stipe as whitish: examination of the best preserved stipe under the binocular confirms this. It certainly lacks blackish dots. The edge of the lamellae is not discolorous. Spores almost geometrically globose, (4) 5·2–5·4 × (3·8) 4·8–5·3 μ; cystidia now more or less completely collapsed; no brown sterile elements seen in the hymenium. Epicutis of pileus consisting of globose to obpiriform cells among which some ampullaceous (obtuse) dermatocystidia were noticed, few dermatocystidia merely fusoid and more or less subacute to acute (but this observation is uncertain because of the collapsed state of the cells); below this there is a hypodermium consisting of horizontal elongate cells and hyphae, both these and the elements of the epicutis with spadiceous pigment which is intracellular and unevenly distributed, not evenly dissolved. No clamp connexions were observed.

This analysis seems to indicate that *P. minutus* is closely related to *P. psychriophorus*. It appears to be one of the numerous forms entering the group called stirps *Psychriophorus* by me, and is treated as a variety of this species in the key.

Pluteus nanellus Murr.

The type from Lake Placid, N.Y. (NY) shows the same anatomical characters as *Leptonia seticeps* Atk. (q.v.) of which it is a synonym. However, Murrill was correct in the generic determination.

Pluteus nanus (Pers. ex Fr.) Kummer (*Agaricus nanus* Pers. ex Fr.)

This species has been given a number of different interpretations, all based, apparently, on Fries's description(*Systema Mycologicum*, **1**, 200, 1821). Since Fries saw living material at that time ('v.v.') and no type material exists in Europe, his description will have to serve as type. Although it is rather probable that this description is based on what is also known as *P. chrysophaeus* sensu Lange and *P. phlebophorus*, there cannot be any proof one way or the other. Under these circumstances it seems best to abandon *P. nanus* as was done for the first time by Kühner & Romagnesi, considering *A. nanus* as *nomen dubium*. The larger form (*A. vascipes* Fr. ad int.) is obviously the same as *P. thompsonii* and would have clear priority had it been published validly.

Agaricus nanus var. *major* Cooke

Obviously the same as *P. thomsonii*.

Agaricus nanus var. *lutescens* Fr.

This variety is almost unanimously interpreted as a representative of this Section, with yellowish stipe, differing from *P. chrysophaeus* sensu Konrad & Maublanc in the colour of the pileus. Only one such species is known in the Northern hemisphere: *Pluteus lutescens* (Fr.) Bres.

Pileus Bracken (M. & P.) to more umber, often with some yellowish lights, macroscopically glabrous but under binocular showing a very fine granular or rivulose discontinuity, smooth or with transparently striate margin (5)–14–40 mm., sec. Kühner & Romagnesi up to 60 mm. broad. *Lamellae* at first paler or brighter lemon yellow, then pink, broad, more or less ventricose, moderately close to close, free. *Stipe* Lemon Y. to Citrin Y. or Brown Sugar, always yellow at first, slightly tapering upward, or equal with slightly subbulbous base, glabrous or subglabrous, 15–40 × 1·5–3·5 mm. *Context* white or pale yellow in pileus, concolorous with surface in stipe, inodorous. *Spores* (5·8) 6–6·8 (7·3) × (4·3) 5–6 (6·5) μ, subglobose, basidia 21·5–27 × 7–7·8μ, 4-spored; cystidia 35–53 (75) × 16–29μ, ventricose-vesiculose or broadly cylindrical usually thickest in middle, always hyaline; cheilocystidia similar, but some smaller and more constantly vesiculose; epicutis of pileus consisting of chains of short cells, the terminal cell usually sub-isodiametric or isodiametric, obpiriform-globose, with light brown to fuscous intracellular pigment (often with pigment condensations), but some cells hyaline, 29–47 × (16) 23–36μ; hyphae of hypodermium hyaline; all hyphae without clamp connexions.

On sandy soil and on rotten wood of coniferous and frondose trees, fruiting in summer and fall. *Caucasus*, Saken, August 1928, Singer (W), on

Fagus orientalis; U.S.A. *Mich.*, Mackinaw City Hardwoods, 6 July 1953, Singer N 406, (F); *Calif.*, near San Francisco, on redwood stump, 1 May 1953, Singer (F). This was also described from Argentina, prov. Buenos Aires, Castelar, July 1948, by A. Martinez (*Lilloa*, **21**, 45–46, 1949). The description refers to the lamellae as initially white which is also occasionally indicated from European material and seems to occur rather frequently. Our material was always yellow-gilled from the start. Numerous European collections by the author coincide with the data given above, but were not preserved.

Pluteus phlebophorus (Ditmar ex Fr.) Kummer (*Agaricus phlebophorus* Ditmar ex Fr.) (Fig. 55)

A type is not preserved, but the description given by Fries, in conjunction with the original plate by Ditmar shows that this is the same species as that described by Lange and Kühner & Romagnesi as *P. chrysophaeus* (Schäff. ex Fr.) Quél. However, the latter was accepted by Fries (1821) as a variety of *P. leoninus*, i.e. with yellowish pileus, and cannot be understood in any other way even though it is true that Fries changed his mind about the characters of this species, attributing to its pileus, in later years, a cinnamon colour saying that (from *P. leoninus*) 'colore constanter differt'.

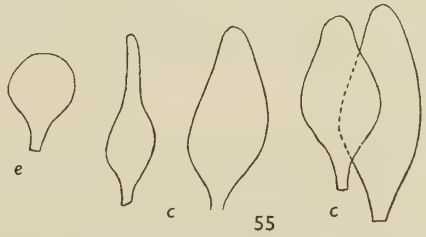

Fig. 55. *Pluteus phlebophorus* from Michigan (Singer N 172). *e*, cell of the epicutis of the pileus, × 500; *c*, pleurocystidia, × 500.

I agree therefore with Konrad & Maublanc who accepted the binomial *P. chrysophaeus* in the sense of the type description, viz. as a species quite different from *P. phlebophorus*. Romagnesi (in Kühner & Romagnesi, l.c. p. 425) considers this species as very close to *P. lutescens*, a correct opinion. It differs however, in the venose covering of the pileus, the deeper brown colour of the epicuticular cells, the lack of umber colour on the pileus. Whether or not this is sufficient to distinguish *A. chrysophaeus* specifically from *P. lutescens*, remains for the European mycologists to determine since the former does not seem to occur in America. But if one of them is considered a variety or form of the other (which at present remains totally unconfirmed), it is *P. chrysophaeus* which has the priority.

As for *P. phlebophorus*, we redescribe the species below:

Pileus cinnamon brown either all over or only in the marginal region (between Cocoa Brown and Alamo, Chestnut, M. & P.), centre very frequently greyish brown (Bracken, Soap Stone, M. & P.), slightly hygrophanous, glabrous but under binocular finely granular-pruinate at times, with smooth disc, more frequently with fine to very strong veins

forming a rugose area or a network which, in extreme cases, occupies almost the entire pileus, with or without transparently striate margin but smooth when dry unless veined, more rarely slightly sulculate when dry, convex, then convex-repand to applanate or slightly depressed, often without umbo, but more often subumbonate, umbonate or papillate, 13–40 (–48) mm. broad. *Lamellae* white, then pink with pink edge, broad to very broad, subclose to close, free. *Stipe* white, or whitish, sometimes sordid striped, or concolorously (with the pileus) innately fibrillose near the base, eventually tending to sordid greyish or sordid buff even if initially white, at least towards the base, rarely remaining whitish when old, sometimes slightly contorted and with an innate subsericeous longitudinally arranged covering, otherwise smooth, but initially often more or less distinctly white pruinose at apex, then glabrous, narrowly hollow or solid, equal or with a slight bulb, 16–55 × 1·5–2·5 mm., base to 4 mm. broad. *Context* white, eventually slightly sordid inside the stipe in most specimens, unchanging otherwise, with a slight acidulous odour, or inodorous. *Spores* 5–8·5 × 4·3–6 (usually 6·5–7·5 × 5·5) μ; basidia 19·5–28 (35) × 9–9μ, 4-spored; cystidia vesiculose or vesiculose-mucronate to broadly fusoid-ampullaceous, always with very broadly rounded apex, rarely with equally attenuate upper portion and subobtuse, sometimes some cylindrical, pedicellate, 40–66 × (7·5) 13·5–21·5μ, hyaline; cheilocystidia similar, but more often shorter: 20–68 × 11–23μ; epicutis of pileus definitely cellular, cells obpiriform, filled with equally dissolved fuscous or brown cell sap; 25–35 × 18–25μ hymenophoral trama inverse; all hyphae without clamp connexions.

On decayed wood of various trees, e. g. *Betula*, *Fagus*, *Salix*, rarely on earth near wood, fruiting from June until fall, northern hemisphere: *Caucasus*, Saken, Kodor, Gwandra, Klytch, August–September, 1928–9, Singer (W); *Leningrad* Region, Georgiewskaya, 17 July 1939, Singer (LE); U.S.A.: *N.Y.*, Cayugà Lake Basin, Van Hook, h.n. 7642, det. Bresadola (as *P. nanus* forma'); 6 Miles Creek, Thom h.n. 15277, 24 July 1903, det. Atkinson (as *P. nanus*), both CU; *Mich.*, Cheboygan Co., Douglas Lake, 23 June 1953, Singer N 106, (F); also N 172, N 192, both (F); Emmet Co., Mackinaw City Hardwoods, 6 July 1953, Singer N 405 (F).

This description of *P. phlebophorus* makes it difficult to separate clearly the *Pluteus satur* Kühner & Romagnesi as keyed out in *Flore analytique*, p. 424, 1953. More data are needed in order to be certain that the latter is specifically different from the former. We have some specimens without venose disc, more velutinous-floccose than most others, with white, more pruinose stipe, and perhaps slightly smaller spores on an average. But we have been unable to draw a sharp line between this and more typical collections.

Pluteus psychriophorus (Berk. & Br.) Sacc. (*Agaricus psychriophorus* (Berk. & Br.) (Fig. 56)

There are specimens of the type collections at Kew and in the British Museum. Spores 5·8–7·3 × 5·5–7·3μ, some geometrically globose, others as elongated as 7·3 × 5·7 (or 6·5 × 6)μ; cheilocystidia light fuscous inside,

broadly cylindrical or ventricose, broadly rounded above; cystidia probably scarce, not studied; epicutis of pileus consisting of a palisade of erect almost hymeniformly arranged dermatocystidioid elements, with some spherocysts or typical obpiriform cells intermixed, yet the majority elongated, 39–48 × 13–16·3 μ, with intracellular fuscous pigment, often in gelatinous condensations, all this above a cutis (the hypodermium). Carpophores small, with campanulate to convex or applanate, umbonate pileus, with fine dense, black, fuzzy fibrils, punctate by these, with rivulose ground, showing white between the tiny crevasses; stipe white.

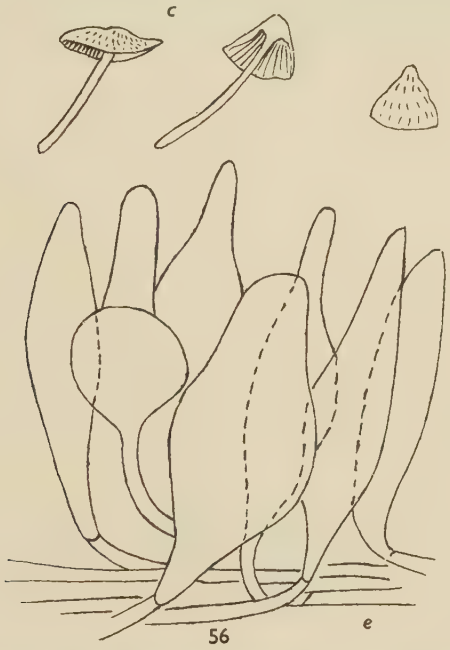

Fig. 56. *Pluteus psychriophorus* var. *psychriophorus*. Type collection, *c*, carpophores, at right a pileus, × 1; *e*, epicutis structure, × 1000.

This species is extremely close to a series of closely related forms such as *P. seticeps*, *P. minutissimus*, etc., and belongs in the subsection with 'mixed' epicutis within which it is remarkable for the reduced quantity of globose elements, absence of veins on striae on the pileus, and white stipe.

Pluteus pulverulentus Murr. (Fig. 57)

The type from Grenada, W.I. (NY) was collected by W. S. Broadway 'on the ground in shade'. Broadway's notes were made from the dried specimens which did not keep Murrill from transcribing them as an original diagnosis. However, luckily, the species is characterized by some microscopical characters which make it unmistakable: spores almost geometrically globose, 4·3–5·6 μ in diameter; cystidia collapsed but apparently

hyaline; epicutis consisting of a dense layer of spherocysts which are filled with pigment condensations or pigment bodies, the pigment rarely evenly dissolved. Centre of pileus rugose, margin non-striate, gill edge pink; stipe was probably white. This species is not rare in Florida, and can be redescribed:

Pileus with a colour resulting from a mixture of 'Saccardo's umber' and 'Pinkish Buff' (R.), disc often very deep sepia brown, with transparently striate to slightly sulcate margin, or smooth, appearing glabrous, but when dried often very finely fibrillose-punctate and rimulose under a lens, very distinctly and constantly venose, radiato-rugose, or reticulate in the centre, campanulate-convex, soon convex and applanate, or sometimes slightly depressed around the umbo, 12–28 mm. broad. *Lamellae* white, then pink

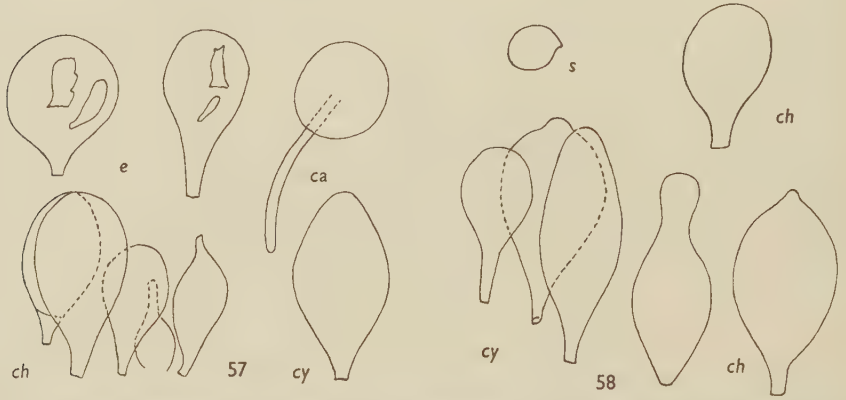

Fig. 57. *Pluteus pulverulentus*. *e*, cells of the epithelium, with pigment condensations in the interior of the cells, × 500; *ca*, carpophore, × ½; *ch*, cheilocystidia, × 500; *cy*, pleurocystidium, × 500.

Fig. 58. *Pluteus rimosoaffinis*. *ch*, cheilocystidia, × 500; *s*, spore, × 1000; *cy*, pleurocystidia, × 500.

including the edge, at first often crowded but at maturity subclose to moderately close, broad, ventricose, free. *Stipe* white, subfibrillose to floccose-tomentose at base, otherwise glabrous, equal or tapering upwards, sometimes slightly bulbous at base 18–32 × 2 mm. *Context* white, unchanging, thin, inodorous. *Spores* 4–6·8 × 3·6–6·4 μ, either all, or at least many, nearly geometrically globose, others subglobose; cystidia ventricose and relatively short or vesiculose, hyaline, very broadly rounded on apex, moderately numerous, 15–49 × 8–25 μ; cheilocystidia short-clavate-vesiculose but some mucronate, 15–50 × 14–33 μ, also hyaline; epicutis of pileus consisting of obpiriform-vesiculose bodies, pedicellate, with gelatinously condensed brown pigment bodies, 35–58 × 22·5–47 μ; all hyphae without clamp connexions.

On very rotten wood of *Ficus* and *Bursera*, etc. in tropical hammock, fruiting in September and October, Florida to Grenada, W.I.: *Fla.*, Dade Co., Matheson Hammock and Royal Palm State Park, Singer F 885, F 1307, F 1327 (all F); *Grenada* (type).

Pluteus reticulatus Murr.

The type from Jamaica (NY) is accompanied by a coloured drawing which shows a medium-sized *Pluteus* with whitish stipe, nearly flat pileus which is brownish fuscous and apparently coarsely reticulate-rugose overall, with non-sulcate margin; lamellae between close and subclose. Spores 5–5·5 × 4·3–5 μ; the anatomy of the carpophore is almost impossible to reconstruct since the specimen is completely permeated with mould hyphae and the hyphae of the *Pluteus* rather thoroughly destroyed. There is, however, an indication in the pattern of the destroyed tissue of the pileus which would suggest that the original structure was cellular, a conclusion likely also because of the strong reticulation of the pileus which is much more common in the species with cellular epicutis than in the Trichodermas. Assuming that the cystidia are hyaline, one would consider this species as closely related to *P. jamaicensis* Murr. from which it differs in larger size, and, if Murrill describes the cystidia correctly, also in the shape of the latter. It is not impossible that the specimens described by Murrill as *P. rimosus* are merely a less reticulate form of *P. reticulatus*.

Pluteus rimosoaffinis sp.nov. (Figs. 58, 59)

Pileo fusco vel badio-fusco in centro vel ubique, margin mox rivuloso et griseo, levi, centro interdum ruguloso, 28–78 mm. lato. *Lamellis* marginem pilei versus debiliter fuscescentibus ad aciem, ceterum roseolis aciemque versus pallidis, confertis. *Stipite* albo, longitudinaliter sulculato, glabro, ad basin bulboso, 33–69 × 4–10 mm. *Carne* alba. *Sporis* 6–6·6 × 5·3–6 μ; cheilocystidiis hyalinis et fuscidulis praesentibus, versiformibus; cystidiis hyalinis, cellulis pilei simillimis; epicute pilei cellulosa, ex cellulis obpiriformibus intus succo fusco vel condensationibus pigmenti repletis. Ad terram, Argentina, Singer T 2011 (LIL) typus.

Pileus fuscous to brown (Chukker Brown to Teak Wood, Santos, English Oak M. & P.) all over or only in the centre, the disc or reticulation sometimes reaching Cordovan (M.& P.), the margin when drying (still fresh) usually cracking minutely to become rivulose and in that zone more grey (Goat, Logcabin, M. & P.), sometimes even with radial coarse rimose stripes, here and in the rivulose zone the white context showing, otherwise extremely finely punctulate dotted (under binocular), macroscopically glabrous in central portion, with very rarely smooth to rugose-uneven and mostly reticulate-venose disc, with smooth to slightly venose margin, convex, then flattened and sometimes concave in age, obtuse or subumbonate, (18) 28–78 mm. broad. *Lamellae* white with greyish-pallid edges, soon pink, with pallid edges, but in a zone about 5 mm. (or less) from the rim of the margin showing pale fuscous-grey edges under binocular, especially when dried, close to crowded, about 5–6 mm. broad, free; spore print dull pink. *Stipe* entirely white, longitudinally sulculate, glabrous, equal or very slightly tapering upwards but with a more or less conspicuous basal bulb (which is 7–13 mm. broad), otherwise 33–69 × 4–10 mm.; mycelium white. *Context* white, unchanging, inodorous. *Spores* 5·5–6·6 × 5–6 μ, from print 6–6·6 × 5·3–6 μ, not geometrically globose but not elongate either, usually about 0·5–0·6 μ longer than broad; basidia about 21·5 × 7·3 μ, 4-spored; cheilocystidia making the edge flocculose

(binocular) and heteromorphous, more versiform than the pleurocystidia, varying from hyaline to light brown (near margin of pileus the majority coloured, otherwise majority hyaline, but coloured cheilocystidia present down to the bases of the lamellae), smooth and thin walled, ventricose to obpiriform-vesiculose, rarely submucronate or subcapitate, 24–93 × 17–48 μ; cystidia obpiriform and often pedicellate, much like the epicuticular cells but all hyaline, smooth, thin walled, moderately numerous, 40–65 × 18·7–33·3 μ; epicutis of pileus cellular, cells obpiriform and often pedicellate, with fuscous intracellular dissolved or brown intracellular colloidally condensed pigment in the same preparation, few hyaline, smooth, 26–57·5 × 16–39 μ; hyphae without clamp connexions.

Figs. 59, 60. *Pluteus rimosoaffinis*. *cA*, carpophore, × 1; *Pluteus rimosus*, *cB*, carpophore from original drawing accompanying the type.

On rich earth underneath a rotting palm trunk, and on palm trunk, shady place, gregarious to fasciculate. Tucumán, Argentina, Singer T 2011, 19 November 1954, type (LIL); T 2012, 25 November 1954, paratype (LIL); 28 January 1955, etc.

This species differs from *P. riograndensis* in being much larger, tending to become rivulose and rimose, having inflated base and less globose spores. Nevertheless, the two species seem to be rather closely related. The poor condition of the type of *P. reticulatus* does not permit a complete comparative study, but the habitat and the smaller spores seem to distinguish it from *P. rimosoaffinis*. *M. rimosus* Murr. shows a large number of similarities, yet I did not see any coloured cheilocystidia or condensed pigment in the epicuticular cells, and the spores are smaller than in our new species.

Pluteus rimosus Murr. (Fig. 60)

The type from Jamaica (NY), Murrill, 214, is accompanied by a coloured drawing. The pileus of the three specimens preserved is non-rimose in two, and rimose in one; therefore, it may be concluded that the rimosity is an exceptional rather than constant character. The spores are short-ellipsoid, 5·5–6·5 × 4·5–4·7 μ; cystidia hyaline, thin-walled, vesiculose; cheilocystidia similar; epicutis consisting of obpiriform cells with fuscous cell sap. Under the binocular one discovers a slight radial venosity in the centre, but observations on fresher material are desirable. Assuming that this is normally non-rimose and somewhat venose, one would be inclined to consider it a synonym of *P. reticulatus* Murr.

Pluteus riograndensis Sing.

The type from Southern Brazil (LIL) was completely described in *Lilloa*, **26**, 116, 1953.

Pluteus roseocandidus Atk.

The type from New York State (CU) was collected by Jackson. It seems to be so little different from another white species, *P. alborugosus* Kühner, in Kühner & Romagnesi, that one wonders if the latter is not a rugose form of the American species. Only further observation in Europe and North America will solve this question. For the time being, we assume that *P. roseocandidus* is constantly smooth, and *P. alborugosus* constantly rugose. See also *P. hololeucus* Sing.

Among other white species, we mention *P. candidus* Pat. which differs in its silky pileus. *Agaricus roseoalbus*, a species often mentioned in European mycological books, cannot be considered as one of the well-known species of the genus. Not a single exact description is available, and the species is much too large for comparison with *P. roseocandidus* Atk. The type of *P. henningsii* Sacc. is probably lost. *P. semibulbosus* (Lasch) Gillet belongs, according to Kühner & Romagnesi to section (*Hispidodermi*) *Trichodermus* Fayod, and Konrad & Maublanc consider *P. candidus* Pat. a synonym of that species. I am thoroughly familiar only with *P. roseocandidus* Atk.

Pluteus rugosodiscus Murr.

The type from Virginia (NY) consists of a fragment of a carpophore in good condition. Spores 6·5–7·2 × 5–5·5 μ; basidia 23–25 × 5·5–8·3 μ; cystidia ventricose or ampullaceous and then with gradually tapering apical neck, obtusely rounded above, thin-walled and hyaline, but most cystidia with a pale melleous resinous incrustation which leaves the apex exposed, often attached to the broadest region of the cell (which is at the middle or below) and making the wall appear thick-walled there, 48–76 × 12·5–15·3 μ; epicutis of pileus distinctly cellular without distinct pigment.

The yellowish green colour of the fresh carpophores, together with the data given above, satisfactorily characterize this species.

Pluteus seticeps (Atk.) (*Leptonia seticeps* Atk.) (Fig. 61)

Two authentic collections were found at CU, one a topo-type (h.n. 18417). They are identical with each other. Spores vary from globose to subglobose 4·7–6 × 4–5·5 μ; basidia e. g. 20 × 6·4 μ, 4-spored; cystidia scattered, hyaline or fuscous inside, ventricose-ampullaceous and pedicellate, thin-walled with broadly rounded entire apex, e. g. 82 × 15·5 μ; cheilocystidia 28–60 × 12–15 μ, ventricose, more rarely clavate to vesiculose, hyaline; epicutis of pileus consisting of a hymeniform layer of vesiculose-piriform cells, interrupted by single or fasciculately aggregated elongated bodies (dermatocystidia); cells isodiametric (e. g. 30 μ diameter) or e. g. 37·2 × 22·8 μ, more or less thin-walled; dermatocystidia moderately thin-walled to rather thick-walled at the apex (1 μ), smooth and entire above, with strongly attenuate apex forming a subacute to obtuse tip but not broadly rounded, usually ventricose below and gradually attenuate upward, or ventricose near middle, with dissolved fuscous intracellular pigment at least in the upper portion, 70–86 × 15–24 μ, rarely as narrow as 8 μ diam.; hyphae without clamp connexions. 'Base often with minute dark scales' (in sched.).

The structure of the epicutis of the pileus is the same here as in *P. longistriatus*, but the two species are very different. On the other hand, this is identical with *P. nanellus* Murr., and so close to *P. psychriophorus* and *P. minutissimus* that it becomes rather difficult to separate these species sharply from each other. The latter two have more obtuse dermatocystidial tips, and, while the variability of the stipe characters is unknown in *P. psychriophorus* (the type has white glabrous stipe), there is a similar variability from white to dark-spotted stipe in the American as well as in the European species. Specimens from the American tropics and subtropics also show such divergent characters as a distinctly sulcate margin, or a strongly venose centre. I am inclined to believe that these are geographical races of *P. psychriophorus*, but their delimitation, even as such, is still difficult as the available material is insufficient. Consequently, I assign them varietal names ad int.:

P. psychriophorus var. *psychriophorus*, see under *A. psychriophorus*.
P. psychriophorus var. *seticeps* (Atk.) comb.nov. ad int., see above.
P. psychriophorus var. *minutissimus* (Maire) comb.nov. ad int. (This was characterized by Maire, Favre, and Kühner & Romagnesi but is unknown to me).

P. psychriophorus var. *dennisii* Sing. ad int.

This is based on Dennis 152 from Trinidad, reported as *P. aethalus* var. *pulverulentus* (Murr.) Dennis but certainly not identical with *P. pulverulentus*. One of my Florida collections (F 366, F), now tentatively determined (in herb.) as *P. rimosus* forma, but different from that species seems very close. Unfortunately, I have not personally studied Dennis's specimen, but rely on the detailed data given by its collector. Moreover, in the case of the Florida collection, I have no data on the fresh material. Dr Dennis kindly

sent me a copy of the colour sketch he made on the fresh material. The *pileus* is pruinose, in the dried Florida material now cracked up into small punctiform wartlets as in the type of *P. psychriophorus*, these deep fuliginous, the general pileus colour in Dennis's sketch is Tiffin to Clove (M. & P.), striate on margin when moist, convex with more declivous margin and soon subumbonate centre, 21–25 mm. broad. *Lamellae* not black-margined, 3 mm. broad. *Stipe* white, but s.l. with tiny blackish specks, dried becoming somewhat fulvescent in some specimens, tapering upwards, pruinose, 23–28 × 2 mm., narrowly hollow, with whitish mycelial pad at base. *Context* white, thin. *Spores* 5–6 × 4–4·8 μ, subglobose (*not* geometrically globose); basidia 18–20 × 8·5–10·8 μ, 4-spored (F 366); cystidia 48–51 × 14–16 μ, melleous-hyaline, ventricose and broadly rounded above; cheilocystidia

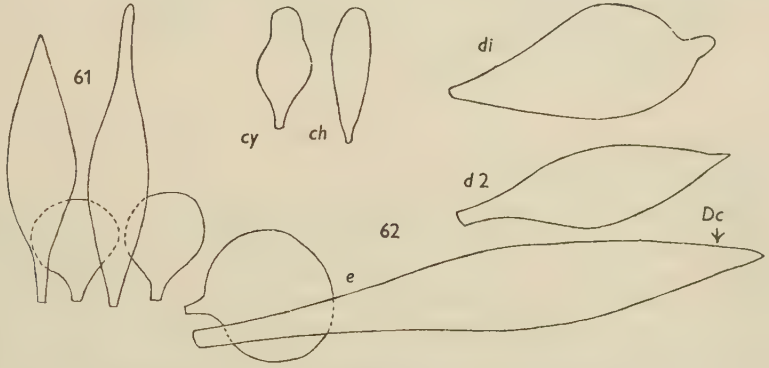

Fig. 61. *Pluteus psychriophorus* var. *seticeps*. Structure of epicutis showing both epicuticular spherocysts and (elongated) dermatocystidia, × 500.

Fig. 62. *Pluteus psychriophorus* var. *burserae*, type collection. *e*, structure of the epicutis of the pileus, with an obpiriform cell and a dermatocystidium (*Dc*); *d* 2, another dermatocystidium; *di*, a cell intermediate between a dermatocystidium and an ordinary epicuticular spherocyst; *ch*, cheilocystidium; *cy*, pleurocystidium. All × 500.

more versiform and of very variable size, generally broadly rounded above, but some with a short mucro; epicutis of the pileus consisting of erect elements forming a subhymeniform layer and of two forms, (1) short obpiriform-vesiculose cells 21–78 × 15·5–36·5 μ, always constituting the majority of the epicuticular cells, (2) among these some more elongate, either broadly ventricose or broadly ventricose-subampullaceous, 48–57 × 14–20 μ (F 366), or subcylindrical, 42–43 × 8·5–8·7 μ (F 366), '160 × 16 μ' (Dennis 152), the longer ones often with a secondary septum (concave to apex); hyphae without clamp connexions.

In swampy forests on rotten logs, fruiting in summer, and until October (Dennis 142), Florida to Trinidad. A specimen from Peru, unfortunately immature, Carpenter no. 154 (LIL) may also belong here.

P. psychriophorus var. *venosus* Sing. ad int. Disc of pileus venose, margin transparently striate (dry smooth), Snuff Brown to Cinnamon Brown (R.). Stipe hyaline, but with fuscidulous cystidioid hairs on lower surface. Spores globose, fewer subglobose, 5·7–6·7 × 5·5–6·5 μ; cystidia on edge and

sides vesiculose, 29–45 × 15·5–29 μ, some with nodules and appendages; epicutis as in *P. seticeps*, cells often with appendages or warts, dermatocystidia relatively not much elongated, 51–68 × 10·8–12 μ; hyphae without clamps. On wood or leaves, Matheson Hammock, Dado Co., Florida 17 October 1942, Singer F 1107 (F).

P. psychriophorus var. *burserae* Sing. ad int. This has granular centre, and relatively long-sulcate margin, it is greyish-chocolate brown, 13 mm. broad; stipe white, on rotten wood of *Bursera*. Spores as in preceding variety; cystidia subampullaceous-vesiculose, e. g. 21·5–32 × 9–13·4 μ, some with excrescences or irregularities; cheilocystidia oblong-subventricose, relatively narrow, hyaline to very pale fuscidulous; epicutis mostly of sub-isodiametric cells with pedicel (22–40 × 21–35 μ), filled with evenly dissolved fuscous pigment, but also numerous fusoid subacute dermatocystidia present, varying from twice as long as the cells to 150 μ and from 11·3 to 21·5 μ in diameter; hyphae without clamps. Matheson Hammock, Dade Co., Florida, Singer F 1462 (F) (Fig. 62).

Pluteus stigmatophorus (Berk. & Br.) Sacc. (*Agaricus stigmatophorus* Berk. & Br.) (Figs. 63, 64)

The type from Ceylon no. 918 (K) was accompanied by a picture now at the British Museum. This again is very closely related to *P. psychriophorus*, *seticeps* etc., and differs mainly in the strikingly black-dotted stipe on brownish yellow ground, slightly larger size. Spores almost geometrically globose, 5·2–5·8 × 4·8–5·8 μ; basidia 4-spored; cystidia filled with fuscous pigment, rather numerous on edge and sides, 10–15·3 μ in diameter; epicutis of 'mixed' structure, with obpiriform cells and fusoid, acute or subacute large (190 × 16·3 μ) dermatocystidia, with dissolved intracellular pigment; hyphae without clamp connexions.

This is very close to what is called here *P. psychriophorus* var. *seticeps* (see under *Leptonia seticeps* Atk.). It may be added to the 'stirps *Minutissimus*' as it is called by Kühner & Romagnesi, temporarily as *P. psychriophorus* var. *stigmatophorus* (Berk. & Br.) comb.nov. ad int. More detailed studies will be necessary in order to decide whether several species can be distinguished within this stirps, mainly on the basis of the degree of black covering on the stipe, the colour and shape of the cystidia, the shape of the dermatocystidia (mostly rounded or mostly subacute), the venosity and sulcation of the pileus, and the average size of the carpophores. For the time being, the best that can be done is an attempt to express the differences among the various types in key form (see below).

Agaricus thomsonii Berk. & Br.

The type from England was studied by Dennis who considers it to be a species of *Pluteus*. I have observed identical material in the Caucasus mountains and I consider the species is conspecific with what was up to now known as *P. cinereofuscus*. The spores are 7–8 × 6 μ, some up to 9·5 × 7 μ; basidia 30–35 × 8–9 μ, 4-spored; cystidia obtuse; cells of the epithelium of

the pileus vesiculose. On dead wood of *Fagus orientalis* and *Alnus incana*. Kühner & Romagnesi find it on the ground and on dead leaves. The grey tinge of the pileus and the size of the carpophores are emphasized in order to distinguish it from *P. phlebophorus*.

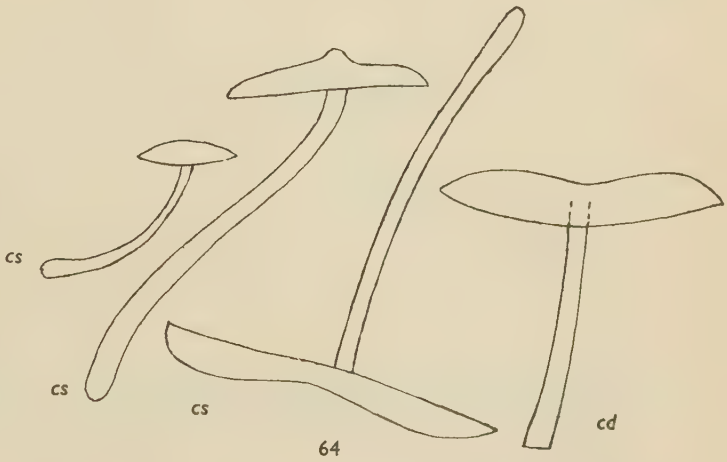

Fig. 63. *Pluteus stigmatophorus*. Epicutis structure with hypodermial cells from which two dermatocystidia and a subisodiametric cell arise, × 500.

Fig. 64. *Pluteus stigmatophorus*. *cs*, carpophores from the dried material as preserved at Kew; *cd*, from original drawing. Both × 1.

Pluteus tucumanus Sing. in Sing. & Digilio (Fig. 65)

Nothing can be added to the diagnosis of the type from Tucumán (LIL, MICH), except that there is a considerable microscopical difference between the form collected at the beginning of the rainy season and that collected at the end of the rains in the autumn. The first of the two had finely mealy stipe, very narrow spores (4–5·5 × 2·8–3·8 μ) and condensed pigment bodies in the epicuticular cells, while the second one has glabrous stipe, broader and somewhat larger spores (5–6·2 × 4–5 μ) and evenly dissolved pigment in the cells of the epicutis. The first of the three characters is not very convincing since the stipe in *Plutei* tends to be glabrescent in age. The spore character may or may not be constant. The early summer form is the type. It is quite possible that future collections will fill in the gap between the two forms, but it is also possible that the early winter form has to be separated from the type. There is also a possibility that the latter is

an extreme form of some other species. The type form of *P. tucumanus* differs from all related species in the small, very narrow spores and the white mealy stipe.

Pluteus umbrinoalbidus Sing. (Fig. 66)

In the type from Southern Brazil (LIL), there is a form with internal pigment condensations (type) and one without them. These are also different in colour, the type being deeper coloured. As in the case of *P. tucumanus*, further studies will be necessary to find out whether both forms are really conspecific. There is a possibility that the rimosity of the pileus is a secondary character rather than a primary one, and that the para-types of both species are actually identical with each other.

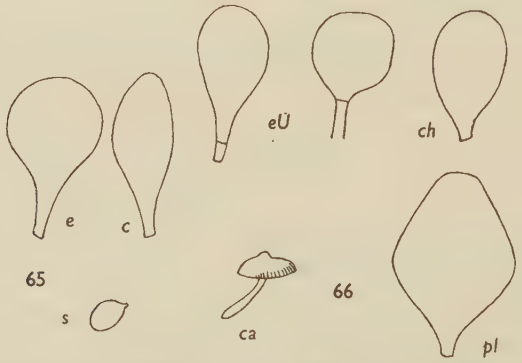

Fig. 65, 66. *Pluteus tucumanus*, collection T 921. *e*, cell of the epithelium of the pileus, × 500; *c*, cystidium, × 500; *s*, spore, × 1000. *Pluteus umbrinoalbidus*, collection B 110. *eU*, cells of the epithelium of the pileus, × 500; *ch*, cheilocystidium, × 500; *ca*, carpophore, paratype, from fresh material, one-half natural size; *pl*, pleurocystidium, × 500.

Pluteus variipes sp.nov.

Pileo fusco vel (aetate) porphyriofusco ('cattail', 'clove Manchu', pl. 8 J 12, demum 'cocoa brown' vel 'Montella' M. & P.), margine primum rivuloso, centro sub lente subtiliter granuloso, dein margine longe pectinato et subrimosello (rimositate in adultis vix notabili, rarius bene visibili), sicco, convexo vel campanulato, dein convexo-subumbonato vel obtuso, demum saepe applanato umbonato exumbonatove, 14–23 mm. lato. *Lamellis* albis, acie concolori, dein roseis, confertis vel subconfertis, latis, liberis. *Stipite* albo, subtiliter fibrilloso in una vel duabus tertiis infernis, ibidem in speciminibus humidis in loco fibrillositate vix discolori, sed statu sicco (nec non exsiccatione) fibrillis griseolis vel fuliginosis obviis, glabrescente, 22–35 × 2–4 mm. (pilei diametro longiore); mycelio basali albo, exiguo vel abundanter strigoso. *Carne* alba, immutabili, inodora, tenui. *Sporis* 4·5–6 × 3·5–5·5 μ, subglobosis, raro piriformibus; basidiis 27–27·5 × 7–7·2 μ; cystidiis voluminosis, 34·7–67 × 16–37·5 μ, hyalinis, ad apicem vel ad basin vel ad ambos membrana incrassata praeditis, rarius tenuitunicatis ad apicem basinque, ceterum tenuitunicatis, ad apicem integris, ventricosis, rarius ventricoso-submucronatis, apice late rotundatis, moderate numerosis; cheilocystidiis simillimis sed ubique tenuitunicatis et minoribus: 30–40 × 13·3–17·3 μ; epicute pilei elementis globosis vel ventricoso-vesiculosis, pigmenti corpusculis brunneofuscis intracellularibus variegatis, 20–44 μ diam., sed interdum pro ratione longiusculis, e. g. 34·7 × 20 μ vel 36 × 22·7 μ; hyphis defibulatis.

Ad truncos vetustos dicotyledoneos in silva subxerophytica vel tropicali litorali, gregatim, Septembri (in Brasilia), Januario (in Argentina), Quebrada de La Higuera (Tucumán) (T 2099, 2100, LIL), Angra dos Reis, est. Rio de Janeiro, Brasiliae (B 432, F). Typus (LIL, T 2100).

The Brazilian collection differs from the type in secondary characters: The base of the stipe is strigose in the tropical form of Angra dos Reis, and the epicuticular cells are less elongated. The type form grew on *Piptadenia*, T 2099 on either *Piptadenia* or an anacardiaceous host; the host of the third collection, B 432, has not been determined.

This species is very close to *P. iguazuensis* but differs from that in the unevenly dissolved pigment of the epicuticular cells; there is also a slight difference in colour, sulcation, spore and cystidia size, and cystidia shape. It is also close to *P. tucumanus* and *P. umbrinoalbidus* which differ in a more rimose than sulcate pileus and permanently white stipe. The four species form a stirps of closely related species in which one may also include the Asiatic *P. albolineatus*.

Species excludendae et incertae sedis

Agaricus alveolatus Cragin is not a *Pluteus*, rather a *Rhodotus*.
Pluteus arenarius Pat. is a *Volvariella*.
Agaricus arenosulus Berk. & Curt. No type at Kew.
Agaricus balanotus Berk. & Br. is probably an immature *Coprinus*.
Pluteus bulbipes Henn. Type probably lost.
Pluteus campanulatus Murr. Type exists. A true *Pluteus*, but *incertae sedis*.
Pluteus candidus Henn. Type probably lost.
Pluteus citrinocarnescens Henn. Type probably lost.
Agaricus curtus Kalchbr. Not a *Pluteus*.
Agaricus cuspidatus Berk. Not a *Pluteus*.
Pluteus deliquescens Murr. Type exists, but in bad condition. This is a *Pluteus*, but *incertae sedis*.
Pluteus giganteus Mass. Not a *Pluteus*.
Pluteus grandis Peck. Not a *Pluteus*.
Pluteus leptonia Rick. A *Rhodophyllus*.
Agaricus marmoratus Berk. Type not preserved. May not be a *Pluteus*.
Pluteus neurodermus Pat. Type not studied, hardly a *Pluteus*.
Agaricus palumbinus Berk. This is a *Pluteus* with spores $7 \times 5{\cdot}3–5{\cdot}5\,\mu$; hymenium destroyed by bacteria; in fact there is little left of the carpophore. There is, however, a good picture in *Icones Hookerianae* where the pileus is depicted umber and subumbonate. It might be possible to re-collect this species at the type locality.
Agaricus pelinus Berk. & Br. A *nomen confusum*. At Kew there are two specimens, one a *Rhodophyllus*, the other doubtful (contains both *Pluteus*- and *Rhodophyllus* spores); the picture at the British Museum (Nat. Hist.) refers, I think, to a *Rhodophyllus*.
Pluteus phlebophoroides Henn. Type probably lost.
Pluteus stercorarius Peck. Hardly a *Pluteus*.
Pluteus sterilimarginatus Peck. Hardly a *Pluteus*.
Pluteus termitum Henn. Not a *Pluteus*.
Pluteus tortus Lloyd. Type not studied.
Pluteus umbonatus Lloyd. Type not studied.
Agaricus wehlianus Müller. Hardly a *Pluteus*.

Other species of *Pluteus*, not indicated in the type studies or in the list of species *excludendae* and *incertae sedis* were either not found in the herbaria where they are supposed to be preserved, or were not readily accessible or available. For European species of this category, see below.

European Plutei excluded from the present revision

The revision of the European Plutei cannot be fully accomplished without a systematic survey of the genus in the regions where the respective species had been described. In many cases, I was not able to throw any new or additional light on species of European origin, when I had to refer to recent European papers (Métrod, Kühner & Romagnesi, and some Czechoslovakian publications, also Lange) where possible. Some species have not been restudied and it is for European mycologists to decide whether they will have to treat them as *nomina dubia*. Those commented on in the type studies, or included in the key following this list, have not been included in this list. Even so, the list is probably not quite complete.

Pluteus argenteogriseus Rea
Pluteus caldariorum Henn.
Agaricus creatophyllus Schulz.
Pluteus cyanopus Quél.
Pluteus diettrichii Bres.
Agaricus ephebeus Fr.
Pluteus floccifer Boud.
Pluteus godeyi Gill.
Pluteus inflatus Velen.
Agaricus kajanensis Karst.
Pluteus luteovirens Rea
Agaricus romellianus Britz.
Agaricus roberti Fr.
Pluteus tenuiculus Quél.
Agaricus melanodon Secr.
Pluteus monticellicus Sacc.
Agaricus occultus Britz.
Agaricus opponendus Britz.
Pluteus phlebophorus var. *marginatus* Qu.
Pluteus pilati Velen.
Pluteus poliocnemus Kühner (nom. subnud.)
Agaricus praestabilis Britz.
Pluteus puberulus Velen.
Pluteus rimulosus Kühn. & Romagnesi (nom.subnud.)
Agaricus umbrinellus Somm.
Agaricus villosus (Bull. ex) Qu.
Pluteus violarius Mass.

Classification

As outlined in the introduction, the classification is basically unaltered in modern treatments, and we still recognize the two Sections proposed by Fayod. Within these, we distinguish Sub-sections which, I am certain, will be called Sections rather than Sub-sections and put side by side with the two basic groups recognized in my *Agaricales in modern taxonomy*. Thus, Kühner & Romagnesi add a third section *Hispidodermi* Fayod which we treat as a sub-section of *Trichoderma* Fayod. Equally, one might prefer to treat the group with elongated as well as subisodiametrical cells in the epicutis of the pileus as a transitory section between *Trichoderma* and *Celluloderma* while we prefer to make it a subsection of *Celluloderma* Fayod. This is at present of minor importance. The following key tends to group the related species of each section and subsection together without the

introduction of new taxa for the respective subdivisional groups. However, for practical reasons, mainly because some characters of some species remain unknown although the species is otherwise well enough known to be recognized as autonomous, the key retains some artificial details that can be eliminated only after further monographic studies. The key also omits certain European species which should be entered in order to make it a 'natural key' rather than a partially natural one, but nothing can be gained by attempting to adapt the experiences of others to the present scheme. The present paper is intended merely to supply data based on type studies and to incorporate these data in a system of classification which is as natural as possible. It should, therefore, not be surprising to find that some European species already described will not key out in the following scheme.

KEY TO THE SPECIES OF *PLUTEUS*

KEY I

A. Epicutis of the pileus exclusively of elongated hyphae, either forming a cutis or a palisade. Section **Trichoderma**
  B. Cystidia of the metuloid type and with inconspicuous to conspicuous horns, prongs, spinules, etc. Subsection **Cervini**, see Key II
  B. Cystidia either not of the metuloid type, and then only rarely with thin-walled inconspicuous nodules or excrescences, or else with slightly metuloid character (walls partially thickened) but then absolutely entire. Subsection **Hispidodermini**, see Key III

A. Epicutis of the pileus exclusively of sub-isodiametrical or vesiculose cells forming a hymenium or epithelium, or, in addition with elongated cells which appear as dermatocystidia. Section **Celluloderma**
  C. Epicutis *with* dermatocystidia. Subsection **Mixtini**, see Key VI
  C. Epicutis without dermatocystidioid elongate elements. Subsection **Eu-Cellulodermini**, see Key VII

KEY II. Section *Trichoderma*, subsection *Cervini*

A. Hyphae with clamp connexions.
  B. Cystidia only with apical prongs.
    C. All cheilocystidia hyaline.
      D. Entire carpophore without pigment. Europe. **P. pellitus**
      D. Carpophore distinctly pigmented.
        E. Stipe, at least in age tending to become blue-green; context of base reacting with phenol; pileus grey, centre dark-squarrose. **P. salicinus**
        E. Not so.
          F. Stipe entirely and exclusively white or pallid, or cystidia thick-walled only at the very apex.
            G. Pileus grey, with dark erect scales in centre; stipe tending to grey at base; cystidia thick-walled only at the very apex. **P. salicinus** var. **achloes**
            G. Pileus umber, fuscous, not fibrillose-scaly, or entire pileus strongly radially fibrillose.
              H. Cystidia moderately numerous or numerous; mostly with 3 or 4, mostly subacute or acute, more rarely obtuse prongs. American species. **P. brunneidiscus**
              H. Cystidia scattered, few, with few obtuse prongs. South Asiatic species. See 'I'.
          F. Stipe with dark innate or superficial fibrils, at least below.
            I. Asiatic species. **P. subcervinus**
            I. American species.
              J. Many clamp connexions present; horns of cystidia short, or horizontal or obtuse *or* stipe deeply fuliginous when dry (and then South American species).
                K. North American. **P. washingtoniensis**
                K. South American. **P. fibulatus**
              J. Few clamp connexions present; horns of cystidia conspicuous, very many of them bifid; stipe *not* deeply fuliginous when dry. North American species. **Pluteus** (Singer N 81, see p. 192)
    C. Edge of lamellae under binocular more or less pale brownish to nearly black; coloured cheilocystidia always present.
      L. Cheilocystidia partly filled with fuscous sap, partly hyaline; edge of lamellae indistinctly discoloured; on *Nothofagus* in Patagonia and Tierra del Fuego. **P. spegazzinianus**
      L. Cheilocystidia all or almost all with deep fuscous sap; edge of lamellae distinctly fuliginous-discoloured; on conifers, perhaps also on *Acacia*, in the Northern Hemisphere. **P. atromarginatus**
  B. Cystidia with lateral prongs. Tropical America. **P. spinulosus**

A. Hyphae without clamp connexions.

M. Cystidia all of the *Cervinus* type or dimorphic; cheilocystidia not all elongate-clavate to clavate-subcylindrical.

N. Edge of lamellae without coloured cheilocystidia, not discoloured.

O. Entire carpophore without pigment. **P. viscidulus**

O. At least the centre of the pileus with fuscous intracellular pigment.

P. All cheilocystidia clavate-vesiculose. Species of the Northern Hemisphere.

Q. Pileus white to greyish pallid in outer region and brown to fuscous on disc; cystidia dimorphic, spores usually small, rarely reaching 8 μ. **P. curtisii**

Q. Not combining *all* the above characters.

R. Pileus small; stipe entirely white; spores 6·5–7·5 (8·5) × 5–6 μ, i.e., small; cystidia of the *Cervinus*-type, few with lateral spinules, with prominent erect sometimes bifid horns. On coniferous wood and coniferous debris on anthills. Europe. **P. cervinus** var. **minor**

R. Not combining all these characters: pileus usually large and stipe, usually at least, with fuscous innate fibrils at the base; spores reaching 8 μ, and often more, in length, i.e., large; cystidia as above, but rarely (and then only very few) with lateral spinules, ordinarily on frondose wood. **P. cervinus** var. **cervinus** (and see note on aberrant form, p. 172, under *A. lilacinus*)

P. Cheilocystidia dimorphic, or a tropical or Southern Hemisphere species.

S. Cystidia characteristically obtusely and shortly pronged or prongs horizontal to recurved; pileus rather deep coloured (Hair Brown to Chaetura Drab (R.)); 20–45 mm. broad; stipe white (sometimes with greyish base) without innate fuscous fibrils; spores 6–9·8 × 5–6·5 μ. Tropical species from South Florida to Trinidad. **P. harrisii**

S. Not combining all these characters.

T. Small to medium-sized form with monomorphic cystidia and (?) cheilocystidia growing in the montane zone. '**P. cervinus** var.' **tucumanensis**

T. Medium to rather large form with often dimorphic cystidia and constantly dimorphic cheilocystidia, South America. **P. xylophilus**

N. Edge of lamellae with coloured cheilocystidia, with fuliginous margin. Patagonia. **P. aporpus**

M. Cystidia not dimorphic, all of the '*Magnus*-type', i.e. often acute, gradually tapering upwards, often with some lateral spines, usually very numerous; cheilocystidia all of the elongated type, i.e., neither short-clavate-vesiculose nor dimorphic in the sense that short-clavate-vesiculose and long-clavate-subcylindrical ones are both making up the non-metuloid elements of the edge (in *P. petasatus* globose but long-pedicellate cheilocystidia not uncommon).

U. Pileus finely innately radially fibrillose-striate; cystidia without lateral and sometimes without apical spines, often thin-walled, especially those at the edge; cheilocystidia elongate but abruptly capitate and broad above, or globose and abruptly pedicellate. On sawdust, straw heaps and dung. **P. petasatus**

U. Pileus not striate; cystidia, at least a large number of them, laterally spiny as well as apically spinose; cheilocystidia all elongate-narrowly clavate to almost cylindrical, often filled with protoplasmatic contents. On wood.

V. Pileus at least 75 mm. broad, often broader. **P. magnus**

V. Pileus 27 mm. broad; stipe 83 × 5·5 mm. **P. ? australis**

KEY III. Section *Trichoderma*, subsection *Hispidodermini*

A. Clamp connexions present.
  B. Stipe dark blue below. Florida. **P. nigrolineatus**
  B. Stipe not dark blue anywhere. **P. avellaneus**
    C. Cystidia with fuscous sap.
    C. Cystidia with hyaline sap (see 'D').
A. Clamp connexions absent.
    D. Stipe, at least in part, pink, pale vinaceous, yellow, cream colour, pale melleous.
      E. Stipe pink or pale vinaceous.
        F. Pileus yellow brown when young, subviscid, centre slightly rugose; cystidia ampullaceous. North America. **P. glabrescens**
        F. Not so. Europe. **P. roseipes**
      E. Stipe yellow, cream colour, pale melleous.
        G. Pileus and stipe pale melleous (see also 'K'). **P. melleus**
        G. Not so coloured.
          H. Terminal elements of epicutis of pileus with broadly rounded apex.
            I. Pileus citrinous with isabelline squamules on disc; stipe cream coloured. Florida. **P. citrinus**
            I. Not so coloured. Tropical Asia.
              J. Pileus grey, margin avellaneous; cystidia almost metuloid but not hooked. **P. conizatus**
              J. Pileus yellowish, often with brown dots, granules, or squamules; cystidia clavate. **P. glyphidatus**
          H. Terminal elements of epicutis of pileus with long-attenuate and mostly subacute apex, voluminous. (Stirps *Leoninus*).
            K. Centre of pileus brown, venose, rugose, or scrobiculate; spores 6·8–7·8 × 5·5–6·5 μ; epicuticular cells filled with a pale ochre-hyaline sap; stipe not permanently white. North America. **P. flavofuligineus**
            K. Not combining all the characters indicated above.
              L. Spores 7–8·5 × 6–7 μ; cystidia 65–100 μ long ventricose-ampullaceous; centre granular-vellereous, gold brown. Europe and Caucasus. **P. sororiatus**
              L. Spores slightly smaller or cystidia slightly shorter.
                M. Terminal members of epicuticular elements from disc with pale fuscidulous contents.
                  N. European species with more or less yellow stipe. **P. luteomarginatus**
                  N. Not so. **P. whiteae**
                M. Terminal members of epicuticular elements from disc with pale yellowish contents. **P. leoninus**
    D. Stipe white or pallid, or else with some discoloration but never pinkish or yellowish.
                  O. Pileus Vinaceous Buff (R.) with black papilla, with fibrillose-pilose surface, with grey hairs, the terminal cells tapering to a thin apex; spores 5·5 × 3·5–4 μ. **P. microsporus**
                  O. Not combining these characters.
                    P. Pileus gold brown, fulvous, yellow, etc.; stipe white; spores 6–6·8 (7·8) × 4·8–5·5 (6·5) μ (see 'N').
                    P. Not combining these characters.

See Key IV

KEY IV. (*Hispidodermini* without unusual colours; cystidia fuscous)

A. Cystidia or cheilocystidia, or both, filled with fuscous sap.
  B. Pileus fawn colour with darker squamose disc; spores 7–8·8 × 5·8–7 μ North America. (Louisiana). **P. squamosidiscus**
  B. Not combining these characters.
    C. Spores 5·7–7·7 × 4–7 μ; terminal elements of epicutis of pileus usually with rounded tips.
      D. Lamellae with dark edge; many cheilo- *and* pleurocystidia coloured (if only cheilocystidia fuscous cf. *P. pusillulus* Rom.)
        E 1. Spores 6·2–7·5 × 4·8–7 μ; carpophores small to medium; Patagonia, Valdivia, Tierra del Fuego. **P. jaffueli**
        E 2. Spores 6–6·5 × 4–6 μ; carpophores medium to rather large. Northern Hemisphere. **P. umbrosus**
        E 3. Tropical South American species, see Key V.
      D. Lamellae not with discolorous edge.
        F. Pileus non-striate or short-striate, granular to furfuraceous-floccose, not radially fibrillose or rimose. Temperate species of Northern Hemisphere (West Indian species. Cf. Key V).
          G. Spores 6·5–9 × 5·5–7 μ, mostly 7–8·5 × 6–6·7 μ. Europe. **P. plautus**
          G. Spores 5·7–7·7 × 4–5·7 μ. North America. **P. granularis**
        F. Pileus either long-striate or fibrillose-rimose as an *Inocybe*, or at least radially fibrillose. Mostly tropical species (except *P. fibrillosus*).
          H. Cystidia with gelatinous pigment condensations inside pileus, radially striped-pectinate; spores 4·8–5 μ broad. **P. multistriatus**
          H. Pigmented cystidia with uniformly dissolved pigment; pileus not as described above; spores broader.
            I. Pileus with brownish cinereous to cinereous radially arranged fibrils, on *Urera*. **P. rimosellus**
            I. Pileus deeper coloured.
              J. Stipe eventually concolorous with pileus in lower third; spores 6–7·5 × 5·3–6·2 μ. Tropical species. **P. subfibrillosus**
              J. Stipe white, glabrous, remaining so; spores 6–6·7 × 5·5–6·2 μ, i.e. shorter than above. Temperate species. **P. fibrillosus**
    C. Spores 4·5–5·5 × 4·3–5·3 μ; epicuticular elements of pileus with subacute free ends. Tropical species.
      K. Spores 5·3–5·5 × 4·8–5·3 μ, globose. Asia. See Key V.
      K. Spores 4·5–5 × 4·3–4·5 μ, subglobose. America. **P. aethalus**
A. Cystidia all hyaline (or melleous from an incrustation), without intracellular pigment. See Key V.

KEY V. (*Hispidodermini* without unusual colours, cystidia hyaline)

A. Epicutis of pileus a trichodermium with the terminal cells dermatocystidioid and with subacute to acute tips, or at least the majority with subacute to acute tips (section from disc of pileus).
  B. Pileus white at least in the marginal zone (see 'F', below).
  B. Pileus not white.
    C. Pileus only 2–6 mm. broad. **P. ? minimus**
    C. Pileus larger.
      D. Spores 5·3–5·5 μ in diameter, globose. **P. escharites**
      D. Spores larger.
        E. American species. **P. fuliginosus**
        E. European or Asiatic species (see 'V').

A. Epicutis of the pileus a trichodermium, or not; if trichodermial, the terminal cells with broadly rounded tips.
    F. Pileus mostly (except sometimes on disc) white, or occasionally with slight pinkish tints in the marginal region.
      G. Stipe near base tomentose from erect fibrils; medium-sized carpophores; North America. **P. tomentosulus**
      G. Not so.
        H. Base of stipe usually bulbous; European species. **P. semibulbosus**
        H. Stipe not so; smaller carpophores.
          I 1. Spores less than 6·5 μ broad; northern-temperate species with minutely furfuraceous or floccose-fibrillose disc and smooth margin, growing on earth and sand. **P. niveus**
          I 2. Spores as above; Argentine species with minutely fibrillose disc, growing on wood. **P. aquosus**
          I 3. Spores 6·5–7 μ broad; West Indian species with glabrous, yellowish disc growing on wood. **P. myceniformis**
    F. Pileus more distinctly pigmented.
        J. Spores small and characteristically elongated; pileus white-silky; North America. **P. unakensis**
        J. Spores broader than 4·3 μ.
          K. Spores 5·3–5·5 × 4·8–5·3 μ, almost geometrically globose; tropical Asiatic species (see 'D', above).
          K. Spores slightly to considerably larger (if only slightly larger, this is an American species).
            L. Spores 5·5–6·5 × 5·8–6·2 μ, almost all globose.
              M. Fibrils of pileus not dense, becoming inconspicuous in age and therefore pileus very pale coloured; elements of epicutis relatively short and broad (see 'BB').
              M. Fibrils rather dense, pileus uniformly coloured or eventually somewhat radially crevassed (minutely); epicuticular elements never very short and broad. **P. nitens**
            L. Spores different.
                O. Cystidia with a persistent loosely incrusting girdle of resinous matter; stipe tending to be cinereous; under Myrtaceae, Patagonia. **P. diptychocystis**
                O. Cystidia not so.

P. Pileus glabrous or with appressed fibrils in the centre, or rivulose or velutinous in the centre, without erect pilose fibrils, without extensive and strongly developed radial appressed fibrils overall, no rimose margin and no distant evanescent floccons overall.

Q. Pileus rather pale coloured, often rivulose, sometimes venose in the centre; odour of *Scleroderma aurantium* or *Lepiota cristata*; epicutis of pileus a trichodermial palisade, but fragmentary; Europe. **P. depauperatus**

Q. Not combining these characters.

R. Spores all more than 6·5 μ broad; pileus appressedly fibrillose, usually relatively large; cystidia broad, more or less vesiculose below and often twice narrowed above (doubly ampullaceous); on Alnus in South America.

R. Spores less than 6·5 μ broad (rarely some giant spores up to 8·7 μ broad); not on *Alnus*, or not in South America. **P. sulcatus**

S. Cystidia ventricose and ampullaceous, or obtuse to subacute at the narrowed tip; pileus hygrophanous, glabrous, or with fibrillose disc, (9) 19–41 mm. broad; North America, south to Trinidad. **P. atriavellaneus**

S. Cystidia broadly clavate to broadly fusoid or broadly cylindrical (with constrictions) or vesiculose, always broadly rounded above; pileus always ± fibrillose in marginal region, often slightly larger than indicated above; West Indies, south to Argentina (see 'X').

P. Pileus not glabrous and without appressed fibrils, sometimes erect fibrils, at least in the centre or when young, or with the fibrils conspicuously radially arranged and tending to show the white trama between them, or with the marginal portion of the cuticle radially splitting-rimose, or becoming so along the elevations of the sulcate margin; sometimes with distant evanescent floccons and fibrils overall, but then usually very pale coloured.

T. Stipe constantly and entirely white or pallid.

U. Pileus fawn colour, with conspicuous erect squamules in the centre; North America (see Key IV, 'B'), or else pileus with conspicuous raised network (see Key V, 'EE').

U. Not combining either the first or the latter alternative combination of characters.

V. Pileus distinctly radially fibrillose over the larger part of the surface, the fibrils often showing the white trama when loosening in age, or completely radially rimose as in some *Inocybes*, or cuticle splitting along the elevations of a sulcate margin.

W. Spores 6–10 × 5–8·7 μ.

X. European species, also Caucasus and North Africa.

Y. Pileus 5–20 mm. broad (see 'CC').

Y. Pileus 30–50 mm. broad. **P. murinus**

X. Tropical, especially neotropical, and subtropical species.

Z. Stipe compressed; Jamaica, W.I. (Cf. *P. compressipes*.)

Z. Not so.

KEY V. (*Hispidodermini* without unusual colours, cystidia hyaline) (*cont.*)

AA. Spores 6·2–8·8 × 5·5–7·3 μ; pileus 17–38 mm. broad; stipe 15–40 × 2·5–3 mm.; margin conspicuously sulcate and often radially splitting above; erect dark spinules in centre always absent. **P. cubensis**

AA. Spores as above, but macrospores up to 10 μ long always present, pileus and the solid stipe both somewhat larger than indicated above, the former with smooth or short sulculate margin and never rimose; erect dark spinules in centre, often well developed (visible s.l. in dry, not dried) condition. (**P. spilopus** var.) **albostipitatus**

W. Spores 5–6 × 4–5·5 μ; Florida. **P. floridanus**

V. Pileus with small floccons or pilose fibrils overall, but not in the manner of the *Inocybes*.

BB. Floccons small and rather distant, consequently pileus rather pale coloured; elements making up the floccons or fibrils generally rather short and relatively thick; tropical species. **P. haywardii**

BB. Not combining the characters indicated.

CC. Tropical species (see 'AA').

CC. Temperate species, often with pilose fibrils, or sericeous fibrils, formed by long cylindrical to slightly fusiform hyphae; Northern Hemisphere, esp. Europe. **P. hispidulus** and **P. exiguus**

T. Stipe either with grey ground colour, or with umber, fuscous, or fuliginous-black innate or free fibrils or floccons, or pale brownish to sordid brown and with hirsute covering.

DD. Pileus and stipe with erect short hirsute pilosity; hairs of stipe often thick-walled; North America. **P. latifolius**

DD. Pileus and stipe not so; tropical and European species.

EE. Stipe with conspicuous blackish-fuliginous spots, dots, or fibrils overall; pileus umbonate.

FF. Cheilocystidia without short attenuate apex, just plainly vesiculose to clavate; Asiatic species. **P. spilopus**

FF. Cheilocystidia with narrowed apex; stipe longitudinally appressedly fibrillose; Argentina. **P. fastigiatus**

EE. Stipe different; pileus umbonate or not.

GG. Stipe white, with occasional brownish fuscous floccons or fibrils at base, see 'X'.

GG. Stipe grey, with white floccons; pileus conspicuously reticulate.

HH. Cystidia absent; Europe. **P. cinereus**

HH. Cystidia present, Florida. **P. cinerellus**

KEY VI. Section *Celluloderma*, Subsection *Mixtini*

A. Lamellae pink, edge brown; cystidia brown; dermatocystidia obtuse. Ceylon. **P. eugraptus**

A. Not combining these characters.

B. Pileus long-pectinate; stipe white; spores subglobose, large: 7–7·8 μ long, 5·5–6·7 μ broad; cystidia hyaline to pale melleous. North America. **P. longistriatus**

B. Not combining these characters. Stirps **Psychriophorus**

C. Pileus venose in the centre. **P. psychriophorus** var. **venosus**

C. Pileus not venose in the centre.

D. Pileus and stipe minute: pileus diameter and length of stipe 3–8 mm. Spores almost geometrically globose, (4) 5·2–5·4 × (3·8) 4·8–5·3 μ. Pileus pulverulent-subpruinate or sericeous, not with black fibrils on white ground. Indo-China (Tonkin). **P. psychriophorus** var. **minutus**

D. Not combining all these characters, and practically always larger than indicated above.

E. Dermatocystidia generally obtuse, with more or less rounded tips.

F. European forms: **P. psychriophorus** var. **minutissimus**

F. American forms and Asiatic type variety.

G. Pileus pruinate, striate; dermatocystidia few. Trinidad. **P. psychriophorus** var. **dennisii**

G. Pileus punctate by dense fine black fuzzy fibrils, very finely white-rivulose; dermatocystidia very crowded. Ceylon. **P. psychriophorus** var. **psychriophorus**

E. Dermatocystidia generally acute to subacute.

H. Entire stipe macroscopically distinctly black dotted; carpophores rather small to relatively large. Ceylon. **P. psychriophorus** var. **stigmatophorus**

H. Stipe white, or at base black-dotted.

I. Margin conspicuously sulcate. On *Bursera* in Florida. **P. psychriophorus** var. **burserae**

I. Margin smooth or inconspicuously sulculate or striate.

J. Many dermatocystidia obtuse; spherocysts in epicutis relatively few (see 'F').

J. Few dermatocystidia obtuse, most of them subacute; cysts in epicutis very numerous. North America. **P. psychriophorus** var. **seticeps**

KEY VII. Section *Celluloderma*, Subsection *Eu-Cellulodermini*

A. Pileus, lamellae, or stipe partly or entirely distinctly yellow to red, or green.
  B. Epithelium hyaline or yellowish.
    C. Spores 4·5–5·5 × 4·3–5·3 μ, almost geometrically globose; pileus orange to orange red. Tropical species. **P. laeticeps**
    C. Spores generally larger, subglobose to ovoid-ellipsoid.
      D. Pileus yellow, golden-yellow. American species.
        E. Pileus rugose-venose in the centre. **P. chrysophlebius** ssp. **chrysophlebius**
        E. Centre smooth. South America. **P. chrysophlebius** ssp. **bruchii**
      D. Pileus yellowish green or orange to reddish orange.
        F. Pileus yellowish green. North America. **P. rugosodiscus**
        F. Pileus orange to reddish orange. North America and Europe. **P. aurantiorugosus**
  B. Epithelium cells filled with brown or fuscous pigment.
    G. Spores almost geometrically globose; many cheilocystidia with fuscous cell sap. Argentina. **P. globiger**
    G. Spores subglobose to short ellipsoid. Stirps **Chrysophaeus**
      H. Pileus fulvous-badious, centre chestnut and venose, diameter 40 mm. Oregon, U.S.A., on earth. **P. fulvibadius**
      H. Not combining all these characters.
        I. Pileus cinnamon, hygrophanous, dry yellow. American species (but perhaps = *leoninus* ss. Romagnesi?). **P. melleipes**
        I. Pileus golden yellow with denser brown granules on disc. European species. **P. chrysophaeus**
        I. Pileus mainly umber. Widespread. **P. lutescens**

A. Pileus, edge of lamellae and stipe free from yellow tints.
  J. Cystidia on edge or sides, or both, with fuscidulous sap.
    K. Edge of lamellae pink (or pale brownish in zone up to 5 mm. from margin).
      L. Spores less than 5 μ broad and pileus radially fibrillose, or spores more than 5 μ broad and pileus glabrous; tropical species.
        M. Spores less than 5 μ broad; pileus radially fibrillose. Ceylon. **P. brunneopictus**
        M. Spores more than 5 μ broad; pileus glabrous, and less than 20 mm. broad. Brazil. **P. riograndensis**
      L. Not with any of these two character combinations, or not tropical. **P. rimosoaffinis** (see also 'O').
    K. Edge of lamellae fuliginous (if merely pale brownish grey and stipe white, see 'L').
      N. Stipe pink. Ceylon. **P. fusconigricans**
      N. Stipe white, fuscous below. Europe, South America, probably widespread. **P. luctuosus**
  J. Cystidia and cheilocystidia hyaline to very pale melleous.
    O. Centre of pileus rugose-venose or rugose-reticulate.
      P. Carpophores entirely white; cystidia very elongated.
        * European species; cystidia 75–115 μ; on the ground. **P. alborugosus**
        ** South American species; cystidia smaller; on wood. **P. hololeucus**
      P. Not entirely white.

Q. Pileus cinnamon brown on the margin or overall, slightly hygrophanous. Europe, Asia, North America. **P. phlebophorus**

Q. Not so coloured.

R. Temperate species (see Key V).

R. Tropical species.

S. Pileus reaching over 40 mm. in diameter. **P. reticulatus**

S. Pileus less than 40 mm. broad.

T. Spores, at least many of them, almost geometrically globose; epicuticular cells with pigment bodies or condensations. **P. pulverulentus**

T. Spores subglobose; epicuticular cells with evenly dissolved pigment. **P. jamaicensis**

O. Centre of pileus not rugoso-venose.

U. Pileus white. North America. **P. roseocandidus**

U. Pileus pigmented.

V. Pileus shaggy, cells of vestiment globose, with solid pigment bodies. Caucasus. **P. keissleri**

V. Not combining these characters.

W. Pileus not tending to become rivulose and rimose, not conspicuously sulcate-pectinate at margin, pileus usually about 30–50 mm. broad. Temperate species.

X. Pileus grey on margin, often brown in centre, but always with a greyish rather than reddish tinge; spores 7–9·5 × 6–7 μ. **P. thomsonii**

X. Pileus with a cinnamon or fulvous tinge, not grey; spores somewhat smaller (see also 'Q'). North American species. **P. ludovicianus**

W. Pileus often tending to become rimose, or at least rivulose and minutely breaking up on the margin so that, when the pileus becomes sulcate at maturity, a more or less radially rimose effect is produced, or else the margin of the pileus distinctly sulcate-pectinate. Tropical and subtropical species.

Y. Pileus sulcate-plicate-pectinate; base of the stipe coloured; rimosity not observed or not conspicuous.

Z. Pigment of epicuticular cells evenly dissolved. **P. iguazuensis**

Z. Pigment of epicuticular cells uneven, with pigment bodies or pigment condensations. **P. variipes**

Y. Pileus at the most slightly and irregularly sulcate in age, and then accentuating a rimosity of the cuticle on the margin which gives it the aspect of an *Inocybe*, more rarely only rivulose, but then not distinctly pectinate all around the margin.

KEY VII. Section *Celluloderma*, Subsection *Eu-Celluloderma* (*cont.*)

AA. Stipe not white; pileus 30–40 mm. broad. Ceylon. **P. albolineatus**
AA. Stipe white. American species (and *P. phlebophorus*, boreal incl. Europe, certain variations).
BB. Pileus 40 mm. broad, or more.
CC. On palm in Argentina (see smooth form of *P. rimosoaffinis*).
CC. Not so.
DD. Jamaica, W.I. (cf. *P. rimosus*).
DD. North America, Europe, etc. (see non-venose, sulcate forms of *P. phlebophorus*).
BB. Pileus never reaching 40 mm. in diameter. South American species.
EE. Epicuticular cells with evenly dissolved pigment (see para-types of the following species).
FF. Pileus only partly rivulose or rimose or becoming so in age; spores 5–6 μ broad; South Brazil. (Cf. *P. umbrinoalbidus*)
FF. Pileus distinctly rimose at maturity; spores up to 5 μ broad. Region of Selva Tucumano-Boliviana. Fruiting in early winter. (Cf. *P. tucumanus*)
EE. Epicuticular cells with pigment condensations and pigment bodies.
GG 1. Pileus only rivulose or with very fine crevasses, not rimose; spores 5·3–5·7 μ broad. South Brazil. **P. umbrinoalbidus**
GG 2. Pileus radially rimose; spores much narrower. Selva Tucumano-Boliviana. **P. tucumanus**
GG 3. Pileus sulcate-pectinate when mature; stipe with greyish fibrils when dry, cystidia larger than in preceding forms (34·7–67 × 16–37·5 μ) (Cf. young carpophores of *P. varipes*).

(*Accepted for publication* 2 *April* 1955)

Trans. Brit. mycol. Soc. **39** (2), 233–238 (1956).

FUNGI OF CHALK SOILS

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The fungal flora of similar horizons in eight different chalk soils was investigated by the dilution plate method. *Penicillium nigricans*, *Mortierella alpina* and *M. minutissima* were abundant in the majority of the soils. Other species, including *Spicaria* sp. and *Paecilomyces* sp., were confined to a single locality. It is suggested that in chalk soils a number of species may be expected to be found and are 'cosmopolitan'. Other species are confined to a particular soil. The distribution of fungi within soil may be similar to the distribution of higher plants on similar soils.

Introduction

In 1931 Jensen suggested that distinct fungal communities are associated with different soils. Recently, Warcup (1951) has demonstrated that in Lakenheath Warren the microflora of the shallow alkaline soils is distinct from that of the deeper, acid, podsols. The list of fungi isolated by Stenton (1953) from Wicken Fen is different from that of Lakenheath Warren. In Wisconsin soils Tresner, Backus & Curtis (1954) found a parallel between higher plant communities and the microflora of associated soils, and that if two plant communities are similar the microflora of the soils may also be expected to be similar to one another.

The aim of this investigation was to determine whether similar chalk soils in widely separated localities support similar fungal floras.

The soils and their localities

The soils examined were alike in overlying chalk, containing larger or smaller particles of chalk, and having a high free calcium carbonate content. All the soils were of alkaline reaction (pH 7·0–8·3) and bore 'chalk' species of higher plants. The soils differed in depth, humus content and detailed vegetation cover, which ranged from undisturbed chalk grassland and woodland to cultivated arable.

Soil A was taken from steeply sloping 'young' chalk grassland near Cudham, Kent. The soil was shallow, about 5 in. deep, with very little organic matter, highly calcareous, and contained many large chalk pieces. The pH was 8·0–8·2. The covering vegetation was composed of *Carex flacca*, *Lotus corniculatus*, *Hieraceum pilosella*, *Viola hirta* and *Camptothecium lutescens*.

Soil B was taken from a gently sloping 'young' chalk grassland from Knockholt, Kent, and was almost identical with soil A. The vegetation cover consisted of *Festuca ovina*, *Potentilla sterilis*, *Poterium sanguisorba*, *Thymus drucei*, *Pseudoscleropodium purum* and *Camptothecium lutescens*.

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Soil C was taken from a shallow, level soil bearing coppiced hazel, near Weyhill, Wilts. The soil was light brown with a small amount of organic matter. It was high calcareous with many small chalk pieces. The pH was 7·0–7·3. The vegetation cover was *Corylus avellana*, *Anemone nemorosa*, *Melica uniflora* and *Viola hirta*.

Soil D was taken from level ground near Westwell, Kent. The ground had been cut away for building purposes and so was slightly disturbed. The chalk rock was about 2 ft. below the surface. The soil was very dark brown, with much organic matter, including dead fibrous roots, but also contained many small chalk particles. The pH was 8·1–8·3. The covering vegetation was *Poa* sp., *Dactylis glomerata*, *Potentilla reptans* and *Acrocladium cuspidatum*.

Soil E was taken from level chalk subsoil which had been exposed in the construction of a garden near Mickleham, Surrey. The soil was grey, with very little organic matter. It contained large pieces of chalk, broken from the chalk rock which was about 9 in. from the surface. The pH was 8·3. The soil at the time of sampling was cultivated and bore herbaceous garden plants, but for 2 years previously it was covered with *Ranunculus repens* and *Aegopodium podagraria*.

Soil F was taken from a gently sloping north facing beechwood near South Harting, Sussex. The soil was light brown, with a limited amount of organic matter, was highly calcareous and contained small chalk particles. The pH was 7·3. The vegetation was composed of *Fagus sylvatica*, *Brachypodium sylvaticum*, *Primula vulgaris* and *Galeobdolon luteum*.

Soil G was taken from level 'old' chalk turf near Mickleham, Surrey. This turf has been undisturbed and ungrazed for 5 years and was developing into *Crataegus*, *Betula* and *Euonymus* scrub until it was checked shortly before soil sampling was carried out. The soil was about 7 in. deep and overlay pure chalk. The soil was dark in colour, contained a high proportion of organic matter and a large number of small chalk particles. The pH was 7·6–7·8. The vegetation cover was composed of *Carex caryophyllea*, *Galium verum*, *Thymus drucei*, *Koeleria gracilis* and *Rhytidiadelphus squarrosus*.

Soil H was taken from the border of a gently sloping arable field near Wolverton, Hants. The soil was light brown in colour, with a limited amount of organic matter, and with a large number of chalk and flint pieces. The pH was 8·2–8·3. The vegetation overlying the soil was composed of *Poa* sp., *Lolium perenne* and *Trifolium repens*.

Soil collection and isolation methods

Samples were taken at comparable depths in each of the soils. The litter layer, where present, was scraped off and a small pit was dug with a sterile trowel. At a depth of 3 in. below the surface a sterile metal container was forced horizontally into the side of the pit. The container was then withdrawn so that it contained a core of soil. No attempt was made to investigate the vertical distribution of fungi in these soils.

Samples were taken over a year at intervals of 2 months from soils A, B, E and G. During this period there was very little fluctuation in the composition of the fungal flora. For the purpose of this paper the results are taken from single samples of the eight soils listed above.

Dilution plates were prepared from 50 g. of each sample of soil, at dilutions of 10^4, 10^5 and 10^6, on glucose-peptone agar, pH 4·4, and malt agar, pH 6·0. For each soil sample a total of twenty-four plates was prepared. The plates were incubated at 25° C. and examined at intervals from 3 to 28 days. Plates with slow growing colonies were kept under observation for 10 weeks or more. All fungal colonies were isolated and maintained in culture on malt or Czapek's agar. Bacteria were not taken into culture.

In addition to the dilution plates, water cultures with split hemp were set up for the isolation of Oomycetes. Soil particles were also plated out on soil extract agar for the isolation of Ascomycetes.

Fungi isolated

In the examination of the soils from the eight sites approximately 800 dilution plates were prepared and the total number of isolates was 206, comprising twenty-six genera and fifty-six species.

No Ascomycetes were isolated either by the dilution plate method or by supplementary plates and plating of soil particles on to soil-extract agar.

A single Basidiomycete isolate which in culture produced tube-like structures round the edge of the plate, was isolated from soil G, but was not maintained in culture.

Six species of Phycomycetes were isolated. *Mortierella* spp. occurred commonly and abundantly. They were isolated readily by the dilution plate method. No increase in numbers or species was obtained by the use of the Chester immersion tube method, or the water culture method using split hemp. Neither did these methods lead to the isolation of any Oomycetes. *Absidia cylindrospora* occurred in five of the localities. It was less common than either *Mortierella alpina* or *M. minutissima*. *Rhizopus stolonifer* and *A. glauca* occurred only once.

The Fungi Imperfecti constituted more than three-quarters of the isolates. *Penicillium* spp. were the most abundant, both in numbers and species. *P. nigricans* occurred in all the soils. The isolates of this species were not identical. They varied in degree of sporulation, colour of colony and of reverse, and in the spore sculpturing. Dr A. H. S. Brown of the Commonwealth Mycological Institute, who has kindly examined a large number of these cultures, considers that the cultures cannot be placed in any other species in the *nigricans* series and that they are best considered together, as *P. nigricans*. *P. thomii* and *P. janthinellum* were also frequently isolated but were not as abundant as *P. nigricans*.

Each of the soils yielded a species of *Phoma*. *Spicaria* sp. and *Paecilomyces* sp. were abundant in the woodland soil C. The isolates of *P. elegans* are not identical but cannot be separated into distinct species. Dr A. H. S. Brown considers that one isolate of *P. marquandii* is intermediate between that species and *Penicillium lilacinum*.

Three species could not be identified as they produced colourless mycelium and no spores.

Throughout the investigation only four colonies of Actinomycetes were observed.

The species isolated and their distribution in the eight soils are given in Table 1.

Table 1. *Distribution of fungi in chalk soils*

	Total number of isolates from single sampling of 50 g. soil							
Soil ...	A	B	C	D	E	F	G	H
Rhizopus stolonifer Fr.	2	.	.	.	.	.	.	.
**Penicillium nigricans* (Bain.) Thom	3	5	3	3	6	4	3	7
P. spinulosum Thom	2	.	.	.	1	.	.	.
(Sterile)	1	.	.	.	.	.	.	.
Mortierella minutissima van Tieg.	1	4	.	3	2	1	4	5
M. alpina Peyr.	.	2	1	.	3	.	.	.
Phoma lingam (Fr.) Desm.	.	2	.	.	.	.	.	.
Cladosporium herbarum Link	.	1	.	1	.	.	.	.
Phoma hibernica Grimes, O'Connor & Cummins	.	2	.	.	.	.	.	.
**Penicillium thomii* Maire	.	1	4	.	.	1	4	2
**P. janthinellum* Biourge	.	.	5	.	.	.	.	8
Botrytis cinerea Fr.	.	.	1	.	.	.	.	.
Penicillium vinaceum Gilman & Abbott	.	.	1	.	.	.	.	.
P. stoloniferum Thom	.	.	2	.	.	.	.	.
Phoma sp.	.	.	1	1	.	.	.	.
Absidia cylindrospora Hagem	.	.	.	1	3	1	2	4
A. glauca Hagem	.	.	.	2	.	.	.	.
Hormodendrum pallidum Oud.	.	.	.	3	.	.	.	.
Stysanus sp.	.	.	.	3	.	.	.	.
**Penicillium steckii* Zaleski	.	.	.	2	.	.	.	.
Verticillium lateritium Berk.	.	.	.	2	.	.	.	.
Synsporium sp.	.	.	.	1	.	.	.	.
**Penicillium chrysogenum* Thom	.	.	.	2	.	.	.	.
P. janthinellum (series)	.	.	.	.	5	.	.	.
Cephalosporium sp.	.	.	.	.	1	3	.	.
Gliocladium roseum Bain.	.	.	.	.	2	.	.	.
**Penicillium frequentans* Thom	.	.	.	.	1	.	.	.
(Sterile)	.	.	.	.	1	.	.	.
**Paecilomyces elegans* (Corda) Mason & Hughes	.	.	.	.	.	2	.	.
Phoma glomerata (Corda) Wr. & Hoch.	.	.	.	.	.	1	2	.
**Spicaria carnea* Duché & Heim	.	.	.	.	.	3	.	.
Penicillium canescens (series)	.	.	.	.	.	7	.	.
**Spicaria griseola* Sacc.	.	.	.	.	.	1	.	.
Trichoderma viride Fr.	.	.	.	.	.	1	.	.
**Paecilomyces marquandii* (Massee) Hughes	.	.	.	.	.	3	.	2
Fusarium sp.	.	.	.	.	.	1	.	.
Penicillium oxalicum Currie & Thom	.	.	.	.	.	.	2	.
Fusarium nivale (Fr.) Ces.	.	.	.	.	.	.	1	.
Pullularia sp.	.	.	.	.	.	.	5	.
Penicillium citrinum (series)	.	.	.	.	.	.	2	.
P. charlesii Smith	.	.	.	.	.	.	1	.
Phoma terrestris Hansen	.	.	.	.	.	.	2	.
Myrothecium sp.	.	.	.	.	.	.	3	.
Penicillium cyclopium Westl.	.	.	.	.	.	.	4	.
**P. decumbens* Thom.	.	.	.	.	.	.	1	.
**Dendrodochium* sp.	.	.	.	.	.	.	.	2
Fusarium lateritium Nees	.	.	.	.	.	.	.	1
Monotospora sp.	.	.	.	.	.	.	.	3
Penicillium terrestre Jensen	.	.	.	.	.	.	.	1
P. cyclopium (series)	.	.	.	.	.	.	.	1
P. miczynskii Zaleski	.	.	.	.	.	.	.	1
**P. lapidosum* Raper & Fennell	.	.	.	.	.	.	.	3
**P. oxalicum* (series)	.	.	.	.	.	.	.	2
Hormodendron sp.	.	.	.	.	.	.	.	3
(Basidiomycete)	.	.	.	.	.	.	.	1
Total number of species recorded	5	7	8	12	10	13	14	16

* Cultures deposited at the Commonwealth Mycological Institute.

Discussion

The fungi isolated suggest that there are a number of species which may be expected to be present in any chalk soil. There are also those species which are less widespread and which are limited to one particular type of chalk soil.

Penicillium nigricans was the most widely occurring fungus in the chalk soils. It has, however, also been recorded from sandy soil (Dale, 1914), chalk and podsol (Warcup, 1951), fen (Stenton, 1953), and woodland (Tresner, Backus & Curtis, 1954). Gilman (1945) gives widespread localities for this species, and Raper & Thom (1949) regard it as widely distributed.

Penicillium thomii was isolated from five of the soils. It is not included in Warcup's list of the fungi from alkaline soils. Hitherto it has been reported mainly from soils rich in organic matter. Stapp & Bortels (1935) found it in forest soil and litter; Stenton (1953) reported *P. thomii* as abundant in the Wicken Fen molinietum. In the present investigation it has been isolated from 'young' chalk soil containing very little organic matter, and has also occurred on 'young' chalk soil dilution plates prepared by other workers in this department.

Among the Phycomycetes *Mortierella alpina* and *M. minutissima* were widespread and abundant. *Mortierella* is considered to be one of the most common genera in the soil (Chesters, 1948), but these two species were the only ones isolated from chalk soils. This is in agreement with Warcup's observation that in the alkaline soils of Lakenheath Warren *M. alpina* and *M. minutissima* 'showed maximum occurrence in or near the chalky boulder clay'.

Absidia cylindrospora was common in five of the soils. It was not isolated from the shallow grey soils A and B.

Of the fungi which occurred less commonly *Spicaria* sp. and *Paecilomyces* sp. were particularly abundant in soil F. Warcup also lists *Spicaria violacea*, *Paecilomyces* spp. and *Penicillium lilacinum* in alkaline soils. Other species which occurred in the chalk soils of the present investigation as well as in the alkaline soils of Lakenheath Warren are *Myrothecium* sp., *Monotospora* sp., *Stysanus* sp. and *Phoma* spp. As a genus *Phoma* was isolated readily from six of the eight localities.

An outstanding feature of the chalk-soil microflora under consideration is the lack of Oomycetes and Ascomycetes. The failure to isolate Oomycetes, even with water culture techniques, may be accounted for in the dryness of the soils and the lack of organic matter.

This latter factor may also account for the lack of Ascomycetes. Warcup isolated two species of *Gymnoascus* from alkaline soils, but none were found in the chalky boulder clay. This, together with the total absence of *Gymnoascus* in the present investigation suggests that this species is unlikely to occur where free calcium carbonate is present in the soil.

A characteristic of the chalk fungal flora is the paucity both of species and numbers compared with the lists given by other workers for fen, woodland, and cultivated soils. This discrepancy is partly accounted for by the absence of Ascomycetes and Oomycetes, and by the fact that a single horizon was investigated in each soil.

It will be seen from Table 1 that not only are *Mortierella alpina*, *M. minutissima* and *Penicillium nigricans* widespread in the soils, but that each of the soils is characterized by an individual fungal flora. Thus in soil D with a total of eleven species there are five species which are confined to that soil. Similarly, soil H has a total species number of sixteen, with ten of these not recorded for other soils. Table 1 shows that the species list increases from soils A to H. It also shows that the increase in the species list is due to the presence of species which are confined to one soil and which occur in addition to the 'common' species.

While it is appreciated that the scope of this present work is very limited, it suggests that in the chalk soils under consideration there are a number of species which may be expected to occur, whatever the nature of the soil, provided that it is derived from chalk. These include *P. nigricans*, *Mortierella alpina* and *M. minutissima*. Each soil, however, contains a number of species which are more exacting in their habitat conditions. It is these species which give individuality to the fungal flora of each soil.

It is suggested that a parallel may be drawn between the fungal flora and the higher plant flora supported by chalk soils. Thus *Penicillium nigricans* and *Mortierella alpina* may be compared to *Lotus corniculatus* and *Festuca ovina* which can be expected to occur on a wide number of chalk habitats. Species such as *Absidia cylindrospora* and *Penicillium thomii* may be compared to *Achillea millefolium* and *Hypericum perforatum* which, though common on chalk, will also be found on widely differing soils. Those species which are confined to disturbed chalk soil (soil E) may be compared to *Clematis vitalba*. *Spicaria* sp. and *Paecilomyces* sp. from beech woodland soil may be similar in distribution to *Cephalanthera* sp. or *Neottia nidus-avis*.

Further work is needed to substantiate these suggestions. It is probable, however, that there is a soil fungal flora of 'cosmopolitan' species and that each soil type is characterized by a number of 'characteristic' species.

I am indebted to Dr A. H. S. Brown for the identification of species of *Penicillium*, *Spicaria* and *Paecilomyces*; also to Mrs M. Turner for help in the identification of *Mortierella* spp.; and to Dr G. Metcalfe for reading and criticizing the manuscript.

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(*Accepted for publication* 5 *September* 1955)

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EFFECT OF SUBSTRATE ON A MICROBIAL ANTAGONISM, WITH REFERENCE TO SOIL CONDITIONS

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(With Plate 5 and 3 Text-figures)

A strain of *Bacillus macerans* having the ability to digest fungal structures was isolated from soil which had been partially sterilized by exposure to propylene oxide vapour. This organism was found to produce in autoclaved soil, the toxic effects observed by the agar film method (Neilson-Jones, 1941) and the cellulose fold method (Dobbs & Hinson, 1953). These two methods and the soil slide methods used here appear to record different facets of the same phenomenon.

The bacterium was tested on different substrates for antagonism towards *Fusarium roseum*. On agar a mutual inhibition could be demonstrated. On this medium and in liquid cultures the fungus eventually became dominant, exhibiting a culturally normal form. In autoclaved soil, after a lag on the part of the bacterium during which the fungus grew and produced typical conidia, intensive lysis of the fungal structures occurred, the fungus retaining its viability largely by means of resting spores. The lag was shown to be a period during which the bacterium becomes adapted to the presence of the fungus. In sand culture, as in soil, the fungus was restricted to a subordinate role. By adding agar or excess liquid to sand cultures the vegetative activity of the fungus could be locally stimulated. The addition of bentonite to cultures did not affect the antagonistic situation or the action of a sterilized toxic medium produced by the growth of the organisms.

The difference between the results from agar and liquid cultures, and those from soil and sand cultures, is an effect of bacterial virulence and not of fungal sensitivity. It is suggested that solid material stimulates the development of a toxic situation through a stereotactic mechanism by providing a large, physically hard surface.

Introduction

The importance of antagonism in the ecology of soil micro-organisms has frequently been stressed. Antagonistic effects observed on artificial media may be unlike those occurring in soil. Commonly an antagonism evident on agar is absent when the situation is studied under soil conditions (e.g. Lewis, 1929; Daines, 1937; Vasudeva, Jain & Nema, 1952; Johnson, 1952); more rarely organisms unopposed on agar show antagonism in soil (Bromfield, 1953; Tveit, 1953).

A desire to understand the effect of environment on the interrelationships of micro-organisms in soil led to an examination of the antagonisms under different conditions between a fungus and a lytic bacterium isolated from the soil.

Materials and methods

Materials

The soil used here has been described by Park (1955). The antagonists *Fusarium roseum* sensu Snyder & Hansen, and *Bacillus macerans* Schardinger, were isolated from this soil. The twelve fungi used in preliminary tests (see Park, 1955) included the *Fusarium* isolate used here. Stock cultures of the two organisms were maintained in tubes of autoclaved soil.

The soil solution used as a culture liquid was obtained by displacement, using sodium chloride as the displacing fluid (Parker, 1921). The synthetic nutrient media used were Czapek's solution (Dox modification) with and without 1·5 % agar. These media were sterilized by autoclaving at 121° C. for 20 min.

Methods of culture

The preparation of soil-dishes for inoculation and examination by contact slides has been described (Park, 1955). Sand cultures in Petri dishes were made by weighing 60 g. dry sand into the dish, sterilizing in the hot air oven at 160° C. for 6 hr. and, when cool, adding 10 ml. sterile nutrient liquid. The sand was first sieved, heated at 160° C. for 4 hr., washed in running tap water for 30 hr., and heated at 160° C. for a further 4 hr. In cultures where powdered agar was used with the sand this was sterilized by standing in contact with 90 % ethyl alcohol for 48 hr. and evaporating the liquid at 35° C. under sterile conditions. The agar was spread over the surface of the sand at the rate of 0·6 g. dish after the nutrient liquid had been added. Bentonite, where used, was added as 1 % weight of sand, and thoroughly mixed before sterilization. Sand cultures in flasks were prepared by adding 15 ml. solution to 75 g. washed sand in a 250 ml. conical flask, which was plugged and autoclaved before inoculation. Evaporation from soil and sand cultures was balanced, when necessary, by the addition of sterile distilled water. No attempt was made to regulate accurately the moisture content of the cultures; they were not, however, allowed to become dry on the surface, nor was the surface unintentionally flooded.

Cultures in small drops of nutrient liquid were made on clean, sterile, glass microscope slides, each supported on a bent glass rod in a Petri dish. A drop (0·2 ml.) of the sterile nutrient was placed in the centre of each slide; 5 ml. of the same liquid was put in the base of the dish to reduce evaporation from the drop. Large bulk liquid cultures were prepared in 100 ml. wide-necked conical flasks, each containing 40 ml. solution.

Cultures were inoculated with the fungus as a conidial suspension in distilled water, and with the bacterium as a cell suspension in distilled water. Inocula were obtained from colonies on Czapek's agar. Sand and soil cultures were inoculated from a fine pipette, the suspensions being evenly distributed over the surface. Liquid and agar media were inoculated using a wire loop. All cultures were incubated at laboratory temperature (16·5–21·3° C.) under varying conditions of daylight.

Methods of examination

Soil and sand cultures were examined microscopically by means of contact slides. Since observation in this way is limited to structures becoming attached to the slide from the surface of the substrate only, the method was supplemented by soil-smear slides. To prepare such a slide a small amount of material to be examined is transferred on a sterile micro-spatula to a drop of water on a clean microscope slide. About 0·1 g. of soil was found to give a suitable preparation; with sand about 0·3 g. was used. The material is comminuted in the water, using the spatula, and the mixture spread over an area of about 1·5 cm. square. The liquid is evaporated at 40° C., and should take not longer than 15 min. After removing the larger particles subsequent treatment is as for the contact slides. Microscopic examination of liquid and agar cultures was made after mounting in lactophenol containing 0·05 % acid fuchsin.

Fungal viability was determined by plating on rose bengal agar (Smith & Dawson, 1944). In the case of soil and sand cultures the plating method described by Warcup (1950) was used. For quantitative determinations of the changes in bacterial and Actinomycete 'numbers' in partially sterilized soil a dilution of 1:100,000 was used, plating in Lipman and Brown's agar: for fungal 'numbers' a dilution of 1:5,000 in Waksman's acid dextrose-peptone agar was used.

The method of Novogrudski (1936) for isolation of lytic organisms was used. Here plates of Czapek's agar and of 3 % malt extract agar on which *F. roseum* had grown for 12 days were inoculated on the aerial mycelium with crumbs of soil about 4 mm. diameter. Replicate series of inoculated dishes were incubated at 25, 20° C. and at laboratory temperature, and examined daily for lysis of the fungus.

Soil treatment

Soil enrichment was carried out in 10 in. plant pots filled with fresh soil and incubated at laboratory temperature. To one set was added a concentrated suspension of viable conidia of *F. roseum*; to a second a duplicate but autoclaved suspension; and distilled water was added to the third set. These additions were distributed over the soil surface in 25 ml. amounts every third day for 24 days. On the 28th day the top 2 in. of soil was sieved, that from each pot being kept separate, and a series of soil dishes prepared from the soil of each pot.

A number of partial sterilization treatments were applied to the soil in the course of the work. These are listed here and numbered for convenience of reference:

1. Fresh garden soil—control.
2. Soil autoclaved 14 days before testing.
3. Soil autoclaved, inoculated with fresh soil, and incubated for 14 days.
4. Soil autoclaved just before testing.
5. Soil exposed for 24 hr. to propylene oxide vapour, 14 days before testing.

6. Soil exposed for 24 hr. to propylene oxide vapour, inoculated with fresh soil, and incubated for 14 days.
7. Soil exposed for 24 hr. to propylene oxide vapour immediately before testing.
8. Soil exposed to ether vapour 14 days before testing.
9. Soil exposed for 24 hr. to ether vapour, inoculated with fresh soil, and incubated for 14 days.
10. Soil exposed for 24 hr. to ether vapour immediately before testing.
11. Soil heated for 1 hr. at 60° C., 14 days before testing.
12. Soil heated for 1 hr. at 60° C., inoculated with fresh soil, and incubated for 14 days.
13. Soil heated for 1 hr. at 60° C. immediately before testing.

Treatments 2–10 were applied to prepared soil-dishes, the volatile antiseptics being added to watch-glasses within the dishes which were sealed during the treatment. The soil in treatments 11–13 was heated in plugged tubes (1 × 6 in.) in a water-bath. Precautions were taken to avoid subsequent contamination during the preparation of the soil-dishes.

Methods of observing toxicity

The quantitative contact-slide method was used for determining lysis. For the agar film method (Neilson-Jones, 1941) the formula of Melin's dextrose agar was modified to: dextrose, 2·0 g.; $MgSO_4.7H_2O$, 0·01 g.; NH_4Cl, 0·05 g.; KH_2PO_4, 0·2 g.; agar, 2·0 g.; distilled water to 0·1 l., the larger quantity of acid phosphate eliminating the necessity for a buffer. Treatments were applied to the soil as described in the previous paragraph, the soil-dishes being prepared with a flat surface. The agar films were prepared by pouring on to the surface of the soil-dish 10 ml. molten agar (temperature 45° C.). The agar was inoculated centrally with a 3·5 mm. diameter disc *F. roseum* culture. Where toxicity was present in the underlying soil the growth from the inoculum, instead of forming a circular colony of dense mycelium, as in controls, was asymmetrical and irregular, formed from tenuous, sparsely branched surface hyphae. Consequently, a subjective classification of the behaviour gave a better indication of the presence or absence of toxicity than did measurements of colony diameter. For the cellulose fold method (Dobbs & Hinson, 1953) the soil-dishes were prepared as in the agar film method. A concentrated conidial suspension of *F. roseum* was spread on one side of 2 in. squares of autoclaved, washed cellulose film (thickness about 25 μ), which were then folded with the conidia inwards. Two folds were placed opposite each other on the surface of the treated soil in a Petri dish in such a manner that part of each fold protruded over the side. Another dish of soil, having received the same treatment, was inverted over the first dish and sharply tapped so that the contents fell, covering the soil already present, and sandwiching the folds between the two layers of soil. The soil was tamped down to achieve the necessary intimate contact between soil and fold. After turning in the protruding edges the lid was replaced. Examination of the conidia in the folds was made after 2 days and after 4 days.

Isolation of the lytic organism

Effect of enrichment on the lytic property of soil

Enrichment of soil with living micro-organisms has been cited by Waksman & Schatz (1946) as a method of increasing the development of specific antagonists. In this experiment the slide-areas of one set of dishes prepared from the enriched soil treatments were inoculated with *F. roseum*, those of another set with *Trichothecium roseum* Lk. Results of conidial counts by the quantitative contact slide method are shown in Table 1. Uninoculated controls gave nil counts for both species. The soil which had received living conidia showed an increased rate of disappearance of conidia subsequently added, even when these were of a species different from that used in enrichment. This appears to be due to a selective stimulation of an antagonistic section of the soil population since in the soil which had been enriched with dead conidia, although there was an increase in the frequency of bacteria on the slides, the subsequent disappearance of conidia was delayed.

Table 1. *Effect of soil-enrichment on the disappearance of added conidia*

Days	Enriched with living conidia	Enriched with dead conidia	Distilled water added
	Fusarium roseum		
0	231*	248	252
2	128	245	150
4	8	60	48
8	0	10	9
12	0	0	0
	Trichothecium roseum		
0	213	195	192
2	124	285	185
4	45	156	115
8	57	157	86
12	19	63	49

* The figures are average numbers of conidia/microquadrat.

The method of Novogrudski (1936) was used in an attempt to isolate the agent responsible for the lysis. Fresh garden soil, soil kept in dishes in the laboratory for 14 days, and soil from each of the enrichment treatments were used as inocula. In no case did lysis of the fungus occur, nor was any growth from the soil particles observed.

Effect of partial sterilization on the lytic property of soil

Winter (1949) has stated that partial sterilization of soil may increase its lytic powers. In the present experiment the treatments numbered 1–13 were applied to the soil, partly in order to find a situation where the lytic agent was retained along with a simplified soil population, thus facilitating identification of the agent.

The slide-areas of all dishes were inoculated with a conidial suspension of *F. roseum*. The results of quantitative observations from contact slides are shown in Table 2. In uninoculated control cultures no *Fusarium* conidia were seen. Re-inoculation of autoclaved soil, carried out by planting small crumbs of fresh soil at regular distances along the slide-area, resulted in a patchy effect, germination and healthy growth and sporulation occurring in some areas of the slides, whereas in others conidial lysis

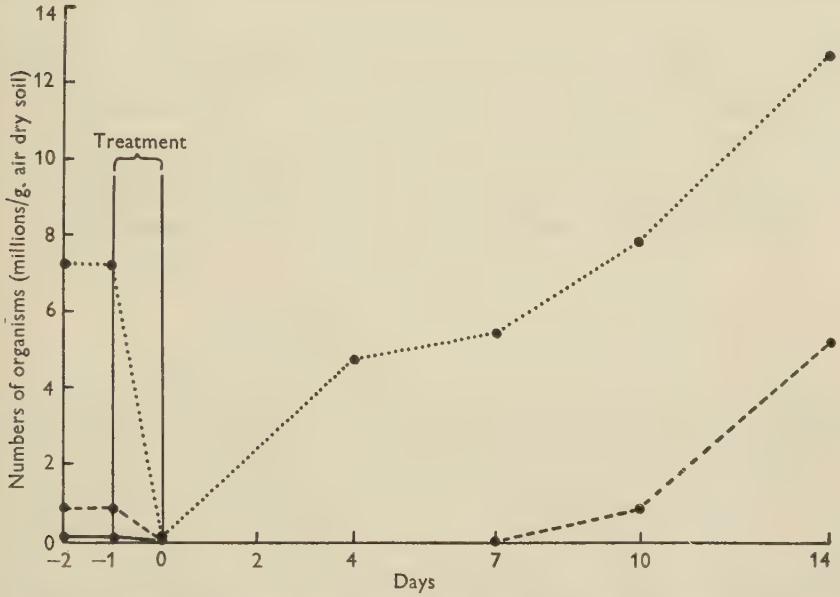
Table 2. *Effect of soil treatment on subsequent development of added conidia*

Treatment no.	Average no. of conidia 0 days	2 days	4 days	Germination of *Fusarium* conidia	Mycelium	*Fusarium* sporulation	Bacterial and actinomycete development
1	115	93	25	−	.	−	+
2	105	61	204, 125*	+++	Healthy	+++	−
3	122	71	84	++	Poor, lysis	+	+++
4	109	24	226, 450*	+++	Healthy	+++	−
5	117	87	40	−	.	−	+++
6	112	101	35	−	.	−	+++
7	120	91	641	++	Healthy	++	+++
8	108	77	62	−	.	−	+++
9	122	64	49	−	.	−	+++
10	113	95	283	++	Healthy 2 days, Lysis at 4 days	−	++
11	120	81	47	−	.	−	++
12	107	78	51	−	.	−	++
13	110	24	900*	++	Healthy	++	++

* Numbers estimated from counts in a measured portion of the microquadrat.
− = nil; + = poor; ++ = moderate; +++ = intense.

was seen. Other fungi in the soil were also subject to lysis in these areas. This result supports the belief that a lytic organism is concerned in the digestion of conidia, the patchy distribution of lysis indicating that the organism spreads rather slowly from the soil inocula. When the soil was partially sterilized (method 7, 10 or 13) the conidia germinated and produced further conidia if added immediately after the treatments. Partially sterilized soils incubated for 14 days before testing showed a return of the lytic factor which was not markedly affected by re-inoculation with fresh soil. The return of the lytic factor in soil exposed to propylene oxide vapour was less rapid than in that exposed to ether vapour, but after 14 days the factor had attained a greater activity following the former treatment. The interpretation put upon these results is that exposure to the volatile antiseptics and to the temperature treatment used reduces the number of micro-organisms in the soil, the resistant species becoming active once more on incubation. Among the resistant forms is one or more which possesses the ability to digest conidia of *F. roseum*. Exposure of soil to propylene oxide vapour was the treatment giving a lytic activity nearest that of fresh soil and was adopted as standard in the work which follows.

The quantitative change in the microfloral population of soil exposed to propylene oxide vapour in Petri dishes was followed (see Text-fig. 1). No fungus survived the treatment. Actinomycete and bacterial 'numbers' eventually increased above those in fresh soil. From the plates on which the counts were made, and from platings in Czapek's agar and in dextrose-peptone agar, isolates of organisms showing different morphological appearances were made. These isolates resolved into eight bacterial forms and one Actinomycete.



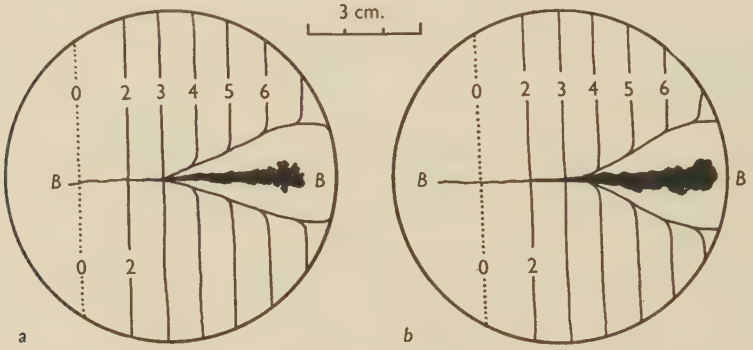
Text-fig. 1. Effect of exposure to propylene oxide vapour upon the 'numbers' of the groups of micro-organisms in soil. ●···●, bacteria; ●– – –● Actinomycetes; ●—●, fungi.

Tests for antagonistic and lytic properties of the isolated organisms

Tests were made against the twelve fungi, poured plates of Czapek's agar being inoculated near one side with the organism under test and then with the fungus at a distance of 4 cm. Control plates were inoculated with the fungus only.

The Actinomycete and six of the bacteria had no appreciable inhibitory effect on fungi, the mycelium growing unchecked over the colonies of the organisms being tested. One bacterium stimulated linear growth of several fungi. The remaining two bacteria both had similar effects. A sharp check to the advancing hyphae occurred at a distance from the bacterial colony, but growth was not completely inhibited. In some species growth of the colony continued at a reduced rate, in others the mass of hyphal tips ceased growth while a few scattered hyphae, described as 'pioneer hyphae', made some growth at a much reduced rate over the intervening zone of inhibition. Distortions of fungal hyphae were common near the antagonistic colonies. The bacteria were identified as *Bacillus macerans* Schardinger, and *B. pumilus* Gottheil.

These two organisms were examined for the property of lysis of fungal structures, the tests being against the twelve fungi. The method used by Meredith (1943) was adopted, mixed suspensions of the appropriate bacterium and fungus being made in melted agar held at 42° C., and poured into Petri dishes. Inoculated in this way the colonies of the bacteria remained small and non-spreading. The fungal mycelium filled the plates except for clear plaques left around the bacterial colonies. In no case was lysis observed.



Text-fig. 2. Effect of colony age on the bacterium-fungus interaction. *B–B*, position of bacterium: 0...0, position of fungal inoculation: the numbers indicate the position of the margin of the fungal colony after successive days. *a* = *Bacillus pumilus*; *b* = *B. macerans*.

In an examination by a different method spores of the fungi were added to melted agar which was poured, the plates being incubated for 6 days, after which time the agar surface had become covered with mycelium. Three large loops of cells of the appropriate bacterium were added to the surface of each plate. No measurable growth of the added bacteria occurred, but the hyphae and spores in contact with the colonies of each bacterium became clear and devoid of pigment. Microscopic examination of these areas showed that some of the structures of the fungi lacked cytoplasm. Lysis at a distance from the bacterial colonies was not observed.

In the experiments now to be described *B. macerans* was used. *B. pumilus*, where tested, was found to be similar in action to *B. macerans*.

Relations on agar

Interaction following discrete inoculation

Poured plates of Czapek's agar were inoculated marginally in a straight line with a conidial suspension of *F. roseum* (Text-fig. 2; 0...0). After incubation at 20° C. for 48 hr. the colony margin had advanced to 2–2. A loopful of bacterial cell suspension was drawn across the surface of each plate, towards, and at right angles to, the advancing fungal hyphae (*B–B*). The plates were incubated at 20° C. and tracings of the development made daily. A composite diagram is shown in Text-fig. 2. The fungus for

the first few hours after the bacterial inoculation was unaffected, and grew over the whole width of the plate. After almost 24 hr. the growing hyphae became inhibited, a clear zone being left between the bacterial and fungal colonies. The zone left in this manner was wider with time as the fungus approached an older bacterial colony, until a maximum was reached. The margin of the fungal colony near the bacterium has been drawn with a clean edge as it appeared the day after its inception. In older regions of the fungal colony, however, the straggling 'pioneer' hyphae described in the initial antagonism test were produced at odd points along the margin, and began to cross the zone. These hyphae were markedly attenuated, showed a contorted growth, and bore terminal and intercalary chlamydospores. Lysis of some of the cells in these hyphae was observed, the chlamydospores in general being less subject to decay than cells of normal form. The bacterial colony was reciprocally inhibited by the fungus, no observable growth taking place where the cell suspension was streaked over the previously formed fungal colony, while maximum growth occurred at the end of the streak away from the advancing hyphae.

Interaction following composite inoculation

A mixed suspension of conidia of *F. roseum* and of cells of *B. macerans* was spread over the surface of each of a series of plates of Czapek's agar. Observations were made of the development on these plates. After 24 hr. the bacterium had formed a continuous colony over the agar surface, and many of the fungal conidia had germinated normally. Growth of the fungus continued, but in some areas unpigmented, translucent patches formed. In these areas lysis of the fungus was intense, structures with staining contents being infrequent and confined to mycelial chlamydospores. Over the remainder of the plates pigmentation was eventually deeper than that shown by pure cultures of *F. roseum* on this medium, although some lysis was observed even in these areas, and chlamydospores were again very numerous (Pl. 5, fig. 1). Aerial mycelium was lacking from the plates for 8 days, when scattered patches of white aerial growth showing normal sporulation appeared and spread outwards over the whole plate. At about the same time the unpigmented areas were colonized from their margins by pigmented subaerial hyphae of culturally normal morphology. After 17 days the plate appeared as though occupied by a pure culture of the fungus. Both organisms remained viable for 21 days, after which observation was discontinued.

Serial subcultivation of the two organisms was performed by taking portions of colonized agar from pigmented and unpigmented areas respectively, macerating in tubes of sterile water, and using the mixture to inoculate fresh plates. Development on all plates prepared in this way was the same as that described, and subcultivation was continued through six series without any observed loss in vigour or mass of either component of the system. Thus on agar a balanced situation exists, the bacterium causing lysis and distortions in the fungus, which can, however, continue its development and even assume a dominant role.

Relations in liquid

Interaction in small quantities of liquid

The antagonism of *B. macerans* towards *F. roseum* was examined in Czapek's solution and in soil solution. The relative times of inoculation of the two organisms were varied: in series (*a*) the organisms were simultaneously added to the drops; series (*b*) was inoculated with the bacterium 48 hr. before inoculation with the fungus; series (*c*) was inoculated with the fungus 48 hr. before the bacterium was added. Observations were made over a period of 10 days.

The fungal hyphae developing in soil solution were more attenuated than those in Czapek's solution; otherwise the development followed the same pattern in both nutrients. Germination of the fungal conidia occurred in series (*a*) and (*b*) in the presence of the bacterium, but subsequent growth of the germ tubes was slow, and the hyphae were narrow and contorted. In series (*c*) a dense mycelium was present before inoculation with the bacterium, but after this inoculation fungal development was retarded, and 4 days after the final inoculation no difference was apparent between the cultures of the different series. Loss of contents of hyphae and conidia was seen from the third day onwards, although fungal growth continued. Chlamydospore formation was common in the hyphae, these spores being generally less subject to lysis than were the vegetative hyphae, although loss of chlamydospore contents did occur. Conidial chlamydospores were formed by a swelling in one or more of the median cells of the conidium, an increase in the granularity of the cytoplasm, and thickening of the cell wall. In all cultures precocious maturity was a frequent phenomenon, an unbranched germ tube, often little longer than the parent conidium, bearing a young conidium at its tip. All stages of maturation of the daughter conidia were seen, from inception to full septation, thus precluding the possibility of misinterpretation of anastomosing germ tubes. Frequently this precocity was carried to such an extreme that no germ tube was evident between the two conidia (Pl. 5, fig. 2). In spore production by budding the cell producing the daughter conidium stained more deeply than the other cells. Behaviour of this sort has been described by Sherbakoff (1915) as the 'Jungkultur' state; it was not observed here in control cultures without the bacterium. At the final observation all cultures contained a large number of normal hyphae with staining contents. Both organisms remained viable.

Thus in small amounts of liquid medium the bacterium readily attacked the fungal structures, digesting portions of the colony, and causing types of development not observed in pure cultures under comparable conditions. In spite of this the fungus remained viable, and structures of culturally normal form were retained.

Interaction in large quantities of liquid

The previous experiment was here repeated using flask cultures. Observations were continued for 21 days.

In Czapek's solution the fungal colonies in the three series behaved similarly. Lysis of some of the hyphae occurred, and chlamydospores and giant cells were formed in the mycelium. No precocious conidial production was seen. The fungal colonies formed floating islands bearing apparently healthy aerial mycelium which eventually covered the surface of the liquid. In soil solution the colonies grew more slowly and remained submerged. Here, as in Czapek's solution, lysis and chlamdospore formation occurred. No unusual methods of conidial production were seen. The relative ages of the organisms had no effect on the final relationship, in which the fungus was dominant. Subcultures of the mixture of the two organisms from the flasks of this experiment into uninoculated flasks of the same medium continued to give the same results.

An important feature was that in both media hyphae of culturally normal form were relatively more common towards the end of the experiment than in the early stages. Pl. 5, fig. 3 shows hyphae of normal form arising from chlamydospores and giant cells. This later production of hyphae having a greater resistance to the toxic environment seems to parallel the finding on agar medium that 'pioneer' hyphae entered the zone of inhibition; and that pigmented hyphae eventually invaded areas of intensive lysis. Christensen & Davies (1940) have reported that a bacterially produced toxin which caused vegetative abnormalities in a fungus was able to induce in it the production of variants better adapted for growth in the presence of the toxin. The pioneer hyphae in these experiments appear to be similar to the ecologically adapted forms described by Brown & Wood (1953), who favour an explanation based on saltation rather than on physiological adaptation.

Relations in autoclaved soil

Dishes of autoclaved soil were inoculated with the bacterium. After 10 days the slide-area was inoculated with conidia of *F. roseum*. Two days later germination had taken place, the germinated conidia differing from those germinating under conditions of pure culture in that they had increased considerably in size, become more deeply staining, and had developed thick walls; the development was in fact of a chlamydosporic nature (Pl. 5, fig. 4*a*). Fungal growth continued and resulted in the production of normal conidia. Lysis was first observed 6–7 days after adding the fungus, and after 9 days most of the mycelium had lost its contents. The groups of newly produced conidia also exhibited stages in digestion. No staining mycelium was found on contact slides prepared after 14 days, and the conidia here were represented largely by empty spore walls (Pl. 5, fig. 5), a few having one or, more rarely, two of the median cells still staining. Contact slides prepared 17 and 21 days after inoculation with *Fusarium* showed no stainable fungal structures. Soil plates prepared at the same time bore colonies of the fungus.

From the twenty-first day onwards the use of smear slides was adopted. In addition, the platings of soil in rose-bengal agar were examined daily under low magnifications of the microscope, and any incipient colonies excised from the plate, excess agar trimmed from them, and the germlings

mounted in lactophenol/acid fuchsin for a more detailed examination. Most of the *Fusarium* colonies on the plates were found to arise from dark-coloured soil particles which obscured their origins. Attempted dissection of these proved successful in a few cases, when it was found that the hyphae originated in whole conidia with swollen cells. Rarely, colonies unassociated with soil particles were formed on the plates, and these also were borne on conidia of this type. On the smear slides, in addition to completely lysed conidia and hyphae, stained structures were found, including both hyphae and conidia (Text-fig. 3). Ungerminated conidia were most frequent, and had their cells swollen, and with dense contents and thickened walls. Conidia of this type bearing germ tubes were seen less frequently, and short pieces of hyphae having a greater diameter than those which were lysed occurred, but were uncommon. All conidia of normal form were devoid of staining contents. Examination of the soil-dishes was continued over a period of 16 weeks without further change being observed, viability of the fungus being retained by means of the structures described. In parallel experiments it was found that inoculating the soil with the two organisms simultaneously, or allowing the soil to become colonized by the fungus first, did not affect the final state attained.

Text-fig. 3. Conidia and mycelium of *Fusarium roseum* after 12 weeks in *Bacillus macerans*-inoculated, autoclaved soil.

It should be noted that the smear slide method differs from the contact slide method not only in enabling the subsurface soil to be examined; it also differs in that the spatial relations of the structures present are disturbed, many soil particles being macerated. If, therefore, the fungal structures remaining viable are in intimate contact with opaque or amorphous soil particles, and there is evidence that this may be so (Thom, 1927), these would tend not to become attached in a free condition to contact slides, and in the presence of the associated soil particle the structures would not easily be seen. On the other hand, comminution of the soil in the preparation of smear slides would tend to detach some of these structures and allow them to lie free.

Lysis as an adaptive phenomenon

The reason for the delay in the action of the bacterium in the previous experiment was investigated. Possible causal factors are: (i) imperfect

colonization of the soil prior to addition of the fungus, due either to insufficient time or to a requirement for the presence of the fungus for effective colonization; (ii) the bacterium having passed its optimum phase and declined in activity; (iii) a time requirement for accumulation of an effective level of a lytic agent; and (iv) an adaptation of the bacterium towards the fungous cell material. The following four treatments of the soil were designed to differentiate between these possibilities:

Treatment (*a*)	Treatment (*b*)	Treatment (*c*)	Treatment (*d*)
Dishes of autoclaved soil inoculated with *B. macerans*	Dishes of autoclaved soil inoculated with *B. macerans*	Dishes of autoclaved soil inoculated with *B. macerans*	Dishes of autoclaved soil inoculated with *B. macerans*
Incubated for 10 days	Incubated for 10 days	Incubated for 10 days	Incubated for 10 days
Inoculated with *F. roseum*	Sterile H_2O added	Inoculated with *F. roseum*	Sterile H_2O added
Incubated for 3 weeks*	Incubated for 3 weeks	Incubated for 3 weeks	Incubated for 3 weeks
Tested for lysis	Tested for lysis	1:100,000 dilution of this soil used to inoculate autoclaved soil-dishes	1:100,000 dilution of this soil used to inoculate autoclaved soil-dishes
		Incubated for 10 days†	Incubated for 10 days
		Tested for lysis	Tested for lysis

Tests for lysis were conducted by inoculating the slide-area with *F. roseum* and following the behaviour by means of contact slides. The results were as follows:

Treatment (*a*)	Treatments (*b*) and (*d*)	Treatment (*c*)
No germination	Germination and sporulation	No germination
Lysis observed after 1 day	Lysis observed after 6 days	Lysis observed after 2 days
No complete conidia after 4 days	Complete conidia present after 11 days	No complete conidia after 4 days

It is seen that in those treatments where the bacterium had previously come into contact with the fungus the onset of lysis was almost immediate, whereas the delay was present in the treatments not having received fungal inoculation prior to testing. The early commencement of lysis in treatment (*c*) precludes the first three possible explanations, thus the action appears to be due to adaptation of the bacterium to the fungus. The maintenance of bacteria in artificial culture may lead to that loss of pathogenicity described as attenuation, and Johnson (1931) has observed that Bamberg's lytic bacterium showed a loss of virulence from the same cause. This effect is probably responsible for the delayed action here. It is not determinable from this experiment whether the adaptation is physiological, in the development of an ability to use the fungus as a substrate, or genetical by selection of virulent strains.

* At the end of this incubation period contact slides showed no fungal structures.

† After this incubation ten dishes of treatment (*c*) were tested for the presence of the fungus, only one giving positive results. It is improbable therefore that more than one of the three dishes used in the test for lysis was infected in this way.

Relations in sand culture

Sand cultures in Petri dishes were prepared, the nutrients being Czapek's solution and soil solution. The dishes were inoculated with *B. macerans* and, after 10 days, with conidia of *F. roseum*. Observations were made by both contact slides and smear slides.

In the Czapek's solution series the conidia had germinated after 2 days, and growth, although less than in controls without the bacterium, was of a normal type. Lysis of hyphae and of produced conidia became apparent after the eighth day, and continued so that after 16 days very little mycelium remained with contents, and no complete conidia were seen. After the twenty-first day only occasional short and contorted lengths of hyphae remained viable. Thick-walled conidia with one or two staining cells were seen more commonly. These stained structures appeared on contact slides with a much lower frequency than on smear slides. This situation was maintained over the 16-week observation period. In the series with soil solution a similar sequence was followed, but after 16 days hyphae were considerably scarcer than in the Czapek's solution cultures. In both media the fungus was reduced to a subordinate role, even when it was added to the culture before the bacterium. These results show more similarity to the condition found in autoclaved soil than to that in agar or liquid cultures, where the fungus eventually became dominant, and viable hyphae and conidia of normal form were usual. The nutrient level in these sand cultures had a slight effect in that with Czapek's solution hyphae were less infrequent than with soil solution. The relatively high frequency of complete conidia and of hyphal pieces in the autoclaved soil cultures of a previous experiment could be due either to a relatively high nutrient status or to the presence of non-solid material which would provide micro-environments more favourable to the fungus.

In a repetition of this experiment parallel series were prepared in which powdered agar was added to the surface before inoculation. Observations over a period of 4 weeks were made by the smear slide method, separate slides being prepared from the surface layer containing agar, and from the deeper material without agar. In both series bacterial development was more intense in the agar layer than in the bare sand-solution layer. In the presence of agar in the sand the behaviour of the fungus was much like that in agar medium cultures, hyphal viability being maintained and a light aerial mycelium being produced. Sporulation occurred in this region, and, although lysis took place, some normal conidia were still viable at the end of the experiment. Examination of the slides prepared from the lower layers of sand showed that here the development followed the pattern described above in connexion with the sand-solution cultures without agar, hyphae being uncommon, and conidia occurring as thick-walled fragments.

In one run of the experiment the surface of one set of dishes was deliberately flooded by the addition of excess of the nutrient solutions. Here, after inoculation and incubation, the excess liquid at the surface bore a mycelial mat of the fungus. In the sand below, however, the situation described for normal sand cultures, in which the fungus was subordinate, obtained.

Effect of culture conditions on bacterial virulence

The experiment was carried out to determine whether the conditions of culture affected the antagonism through bacterial virulence or through fungal activity. Preliminary experiments showed that the toxic factor present in a *B. macerans* culture medium did not pass a Seitz filter pad. The toxic solutions required were therefore sterilized by autoclaving. Czapek's medium was used as the nutrient, in one series as liquid in flasks, in the other series as sand culture in flasks. In each series one set of flasks was inoculated with *B. macerans*, another set with both *B. macerans* and *F. roseum*. The cultures were incubated at laboratory temperature for 12 days. Each batch of 'spent medium' was then filtered through paper and autoclaved in 50 ml. lots at 115° C. for 15 min. The solutions were found to give no growth when samples were plated on agar. The change in pH of the solutions due to growth of the organisms is shown in Table 3.

Table 3. *Effect of growth upon the pH of Czapek's solution*

	Liquid culture		Sand culture	
Original solution	*Bacillus* alone	*Bacillus*+ *Fusarium*	*Bacillus* alone	*Bacillus*+ *Fusarium*
6·8	6·6	6·5	6·6	6·6

It is understood that autoclaving a bacterial cell suspension in this way may release into extracellular solution toxic substances not normally diffusing out of the cells; on the other hand the process may have a destructive effect upon antifungal substances present. Thus from this experiment no conclusions about the actual level of fungitoxic substances produced by the bacterium can be drawn. However, since all the media were subjected to the same treatment, the results are a criterion of the relative virulence of the bacterium under the different conditions of culture. Each sterilized 'spent medium' was tested for its effect on the fungus both as drops on slides, and in sand culture in Petri dishes. The conditions of test had no effect on the reaction of the fungus to the medium, i.e. the sensitivity of the fungus was similar in liquid culture and in sand culture, the results will therefore be described with reference to the effects of the different 'spent media'.

The liquids obtained from both the liquid cultures acted similarly, conidial germination being normal (85–90 %) and growth leading to dense colonies, sporulating abundantly. No lysis was observed, and distorted hyphae, though present, were very infrequent. In the sterilized liquid from the pure bacterial culture in sand 73 % of the conidia had germinated normally after 24 hr. Subsequent growth was slower than that in controls, and giant cells and chlamydospores were rather frequent in the mycelium. The fungus eventually produced a sporulating mycelial mat which covered the surface. The sterilized liquid from the sand culture in which both organisms had grown had the greatest effect on the fungus. Germination averaged 18 % after 24 hr., the germ tubes being commonly contorted, and some showing precocious sporulation. Chlamydospore

formation in the cells of both germinated and ungerminated conidia was a common phenomenon. Growth continued throughout the 10-day period of observation, but even at the end of this time the colonies were extremely tenuous. Thus the degree of toxicity exhibited by the sterilized culture liquids, and hence the virulence of the bacterium towards the fungus, was markedly affected by the conditions of culture of the bacterium, optimum toxicity being obtained when the two organisms were grown together in sand culture.

Effect of colloidal material on the relationships

Soil differs from sand-nutrient solution in that it contains colloidal material. Certain sorts of antifungal substances may be inactivated by adsorption on to colloidal material in soil (Gottlieb, 1952), or on to bentonite in sand culture (Skinner, 1953).

Effect of bentonite on antagonism

The interaction between the two organisms was examined in sand + bentonite culture, with Czapek's solution and soil solution as the nutrients. Controls were without bentonite. Apart from the fact that bacterial cells were much more frequent on slides prepared from cultures with bentonite than on those from controls, the behaviour was the same in both treatments. Fungal development was identical with that described for the corresponding cases in the sand culture experiment, showing that bentonite had no ameliorating effect on the antagonistic situation.

Effect of colloidal material on the toxicity of the 'spent medium'

A toxic liquid was prepared by growing together *B. macerans* and *F. roseum* in sand culture and autoclaving the filtrate at 115° C. for 15 min. This liquid was added to sterilized sand + bentonite in Petri dishes. Control cultures were without bentonite. No difference was observed between the behaviour of conidia of *F. roseum* added to the two cultures, the liquid in both being toxic and affecting fungal behaviour as described.

Dry autoclaved soil brought to 45 % water holding capacity with the sterilized 'spent medium' was also toxic to added conidia of *F. roseum*, the phenomena observed in sand cultures occurring. The toxic principle is thus active in the presence of colloidal material.

Comparison of the lysis with other observed toxicities

The effect on the lytic powers of a soil of some of the partial sterilization treatments applied in an earlier experiment are reminiscent of some results of other workers. Neilson-Jones (1941) found that the toxicity to fungi of Wareham Heath soil was removed by autoclaving, or by exposure of the soil to the vapour of volatile antiseptics. He demonstrated the return of the toxicity after inoculating autoclaved soil with fresh soil. The fungistatic factor investigated by Dobbs & Hinson (1953) also disappeared when the soil was autoclaved, heated at 60° C. for 1 hr., or exposed to an antiseptic

vapour. After the latter treatment the freedom from toxicity lasted but a few days. The experiments in this section were carried out to determine how closely these toxic factors are related.

Toxicity of partially sterilized soil

The contact slide method, the agar film method, and the cellulose fold method were used to observe lysis, inhibition of mycelial growth, and inhibition of conidial germination, respectively, as these phenomena were affected by the thirteen treatments used previously. The results obtained are shown in Table 4.

Table 4. *Effect of soil treatment on the toxicity of the soil as observed by different methods*

Treatment no.	Contact slide method: Percentage original inoculum		Cellulose fold method: percentage germination		Agar film method: mycelial growth
	2 days	4 days	2 days	4 days	
1	71	21	0	0	Tenuous
2	30	170,000*	94	*t*	Good
3	88	35	53	*t*	Nil†
4	37	215,000*	93	*t*	Good
5	79	34	0	0	Tenuous
6	91	32	0	0	Tenuous
7	75	536	89	*t*	Good
8	70	54	0	0	Tenuous
9	51	42	0	0	Tenuous
10	82	373	91	*t*	Good
11	68	43	0	0	Intermediate
12	73	49	0	0	Intermediate
13	28	1,020*	89	*t*	Good

* Estimates of total numbers from measured portions of the microquadrat.
t = tangled growth–counts impracticable.
† See text explanation.

Treatments 2, 4, 7, 10 and 13 were favourable to fungal development as recorded by each of these three methods, while treatments 1, 5, 6, 8, 9, 11 and 12 were unfavourable. In treatment 3, re-inoculated autoclaved soil, the result expressed by the cellulose fold method was similar to that given by the contact slide method in that complete inhibition occurred in some areas, whereas in others the percentage germination was high. In treatment 3 of the agar film method no *Fusarium* could be seen, the agar being rapidly obscured by a profuse aerial mycelium of a mucoraceous nature. The experiment confirms that the phenomena observed by the three methods are affected in similar ways by the action upon soil of the experimental treatments.

Dobbs & Hinson (1953), using the cellulose fold method, found that the fungistatic factor did not return to autoclaved soil which had been inoculated in an unspecified manner with fresh soil, and incubated. The lack of agreement between their result and that obtained here may be due to the method of re-inoculation being different. In the present work a

number of point inoculations were used, giving the composite result described. Alternatively, the generally similar results may be produced by different agents in the two cases.

Toxicity of Bacillus macerans-*inoculated autoclaved soil*

It was earlier shown that the situation in normal soil, where conidia are digested, can be simulated in autoclaved soil by inoculating with *B. macerans*. This experiment was carried out to determine whether this is so with the phenomena expressed by the other methods of observing toxicity.

Dishes of soil with a flat surface were autoclaved at 121° C. for 30 min., cooled, inoculated over the surface with the bacterium, and incubated for 10 days. Dishes were tested for inhibition of germination by the cellulose fold method, and for toxicity towards mycelial growth by the agar film method. Another series of dishes was treated similarly, but after the 10-day incubation period was further inoculated with *F. roseum* and incubated for 21 days before being tested. Controls without the bacterium were used. Table 5 shows the results obtained. Complete inhibition of

Table 5. *Effect of* Bacillus macerans *in autoclaved soil upon the toxicity of the soil to* Fusarium roseum

Autoclaved soil	Cellulose fold: percentage germination after 2 days	Agar film: mycelial growth
Inoculated with *B. macerans*	76	Good
Inoculated with *B. macerans* + *F. roseum*	0	Tenuous
Uninoculated	91	Good
Inoculated with *F. roseum*	87	Good

conidia in the cellulose folds was obtained only in soil inoculated with both organisms; similarly, in the agar film method, over this soil only was the mycelium affected to a degree comparable with that over normal soil. It thus seems probable that the three methods, as used here, reveal different facets of the same antagonistic situation. The fact that complete inhibition of conidia in the cellulose folds occurred in inoculated autoclaved soil in this experiment supports the conclusion arrived at earlier, that a diffusible extracellular toxin may be active in the soil in the presence of colloidal material. Further, the action of toxic soil on mycelium growing on agar above the soil is confirmatory evidence that the difference between solid and non-solid substrates derives from their effect upon the virulence of the bacterium rather than upon the sensitivity of the fungus.

Discussion

From the deliberately simplified conditions presented in this work an attempt has been made to understand some of the factors operative upon micro-organisms as they live in the soil. The metabolic products of the bacterium grown in pure culture under conditions approximating to those of soil showed little toxicity towards the fungus, yet the substances pro-

duced when both organisms were grown together under these conditions were highly toxic. This effect is attributed in part to adaptation of the bacterium to the presence of the fungus; however, the possibility that the fungus itself contributes to its own destruction cannot be discounted. In fact, lysis of one organism by another may be brought about by an increase in the intensity of staling, and hence of autolysis, in the sensitive organism. Thus, in the view of the author heterolysis and autolysis need not be mutually exclusive mechanisms.

A marked difference occurred between the interaction of the organisms on normal laboratory media, and that in sand and soil cultures, the fungus being dominant in the first type of habitat, whereas in sand and soil cultures it was reduced to a largely inactive condition. While the nutrient status had some influence on the activity of the fungus in these situations, this factor cannot account for the difference, since the same solutions used in the different habitats gave different results. The possibility of soluble substances in the sand causing the effect is ruled out by the dominance of the fungus in agar added to sand cultures, and in free liquid above sand cultures. Brown (1923) points out that staling is more marked under conditions of reduced aeration, and where the culture medium is used in shallow layers. From the experiments described here there was no evidence that these factors separately affected the situation. However, in sand and soil cultures the liquid is present as shallow films about the soil particles, and gaseous diffusion will be restricted within the pore space of the substrate. This combination of the two factors may tend to favour the development of a toxic situation.

A further possible factor in the increased toxicity in soil and sand cultures is suggested by the comment of ZoBell (1949), that many soil bacteria grow preferentially upon solid surfaces. In the present work bacterial numbers appeared to be higher in agar and liquid cultures than in sand cultures. However, the presence of solid material may affect physiological activities other than cell growth and division; for instance, Quastel (1955) states that in soil many types of metabolism occur entirely at the surface of soil particles. Following this interpretation of the increased toxicity as a stereotactic phenomenon, connoting a stimulation through contact with a solid surface, it would appear that powdered agar added to sand cultures allows mycelium to remain viable by providing a physically favourable habitat for the fungus. In soil, partly decomposed plant debris could act in the same way, as distinct from any nutrient effect, and may thus protect dormant structures of species no longer able to utilize the changed material as food.

I should like to express my thanks to Prof. C. W. Wardlaw for his interest and encouragement, and for advice in the preparation of the manuscript; to Mr E. Ashby for undertaking the photographic work; and to Dr D. G. Evans, who identified the bacterial isolates.

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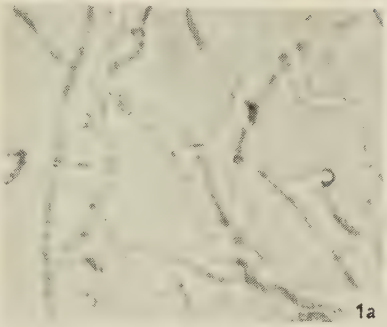
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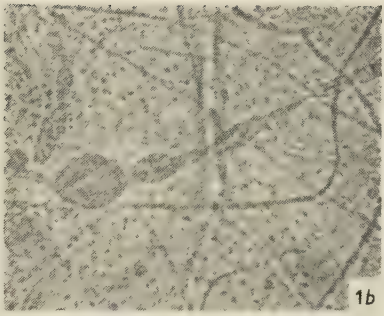
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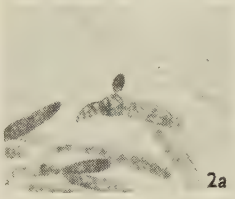
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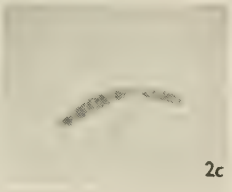
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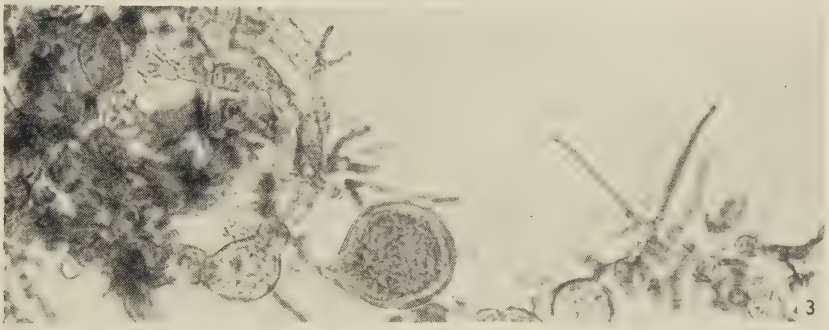
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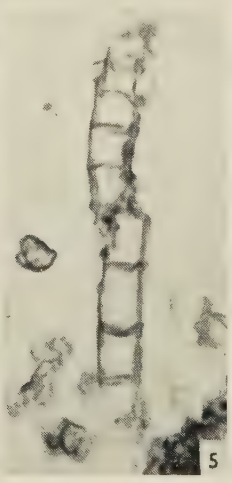
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EXPLANATION OF PLATE 5

Fig. 1 *a*, mycelium of *F. roseum* in pure culture on Czapek's agar, × 1000; *b*, mycelium of *F. roseum* in the presence of *B. macerans* on Czapek's agar, × 1000.

Fig. 2 *a*, early stage in the lateral budding of a conidium, × 440; *b*, later stage in lateral conidial budding, × 440; *c*, terminal budding of a conidium, × 440.

Fig. 3. *F. roseum* grown in the presence of *B. macerans* in Czapek's solution, showing chlamydospores and giant cells. Hyphae of culturally normal form have begun to grow out from some of the giant cells, × 440.

Fig. 4 *a*. *F. roseum* conidium having germinated in *B. macerans*-inoculated soil, showing chlamydosporic development, × 1000; *b*, *F. roseum* conidia on addition to soil, for comparison with 4 *a*, × 1000.

Fig. 5. Completely lysed conidia of *F. roseum* from *B. macerans*-inoculated soil, after 14 days, × 1000.

(*Accepted for publication* 6 *June* 1955)

Trans. Brit. mycol. Soc. **39** (2), 260 (1956).

BRITISH RECORDS, 12

12. **Pleurage perplexens** (Cain) C. Moreau, *Les Genres Sordaria et Pleurage*, p. 264, 1953.

A species of *Pleurage* developed on rabbit pellets from Dipton Wood near Newcastle in 1949 and was isolated on rabbit-dung agar. It agreed with Cain's original description except for the absence of the long, slender flexuous, hyaline hairs covering the perithecium. Later, however, these were found to develop when the fungus was grown, at Dr Cain's suggestion,

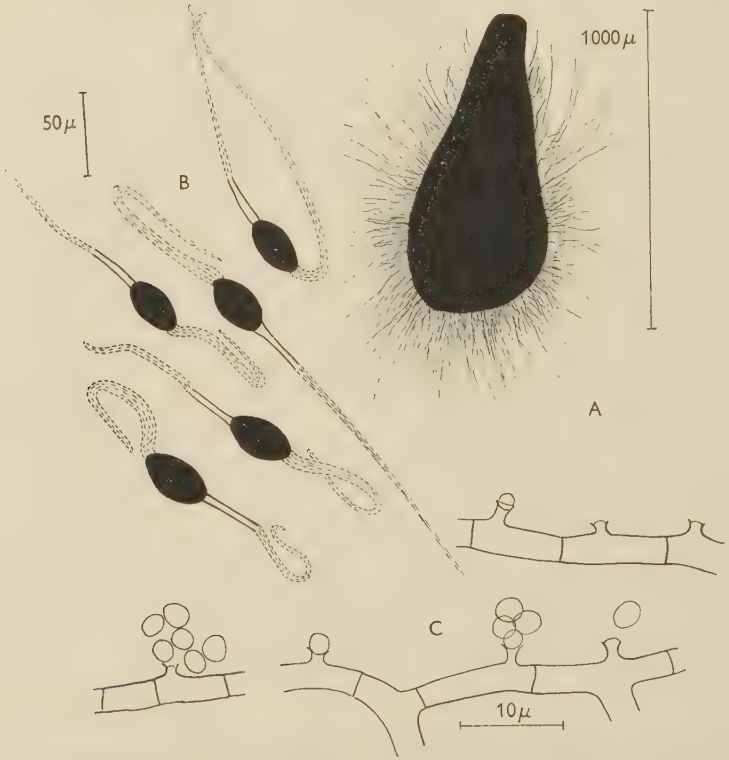

Fig. 1. *Pleurage perplexens*. A, perithecium developed on soil agar; B, freshly discharged ascospores; C, mycelium producing microconidia.

on soil agar. A number of single-spore cultures fruited, showing the species to be homothallic. In culture the mycelium grows flat on the agar and ripe perithecia take 4–6 weeks to develop. An unusual character is the presence of abundant microconidia forming plainly visible white masses on the culture. Cultures have been sent to Commonwealth Mycological Institute, Kew

WINIFRED M. PAGE, Birkbeck College (University of London).

Trans. Brit. mycol. Soc. **39** (2), 261–266 (1956).

SOME INOPERCULATE CHYTRIDS FROM SOUTH WALES

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(With Plates 6 and 7 and 5 Text-figures)

Rhizophydium mammillatum, *R. constantineani*, *Entophlyctis confervae-glomeratae*, *E. bulligera*, *Cladochytrium replicatum*, and *C. aurantiacum* sp.nov. are recorded from fresh waters in South Wales.

C. aurantiacum is characterized by orange-coloured mature zoosporangia, a large orange globule in the zoospore, and sparse large hyaline spindle-organs on the fairly coarse and profuse rhizomycelium.

During the years 1949–50 a routine search for chytridiaceous organisms was made in several ponds and streams in the region around Cardiff. Attention was focused mainly on the saprophytes because in Britain this group, rather than the parasites, has been the more neglected. The methods adopted in the investigation were based on those outlined by Couch (1939) and the occurrence of two inoperculate species (*Diplophlyctis intestina* and *D. laevis*) has been mentioned in an earlier paper (Richards, 1951). This paper notes six other inoperculate species (four monocentric and two polycentric), of which one appears to be new and is diagnosed as a species of *Cladochytrium*.

Rhizophydium constantineani Saccardo

This species was found on dead cells of *Oedogonium* sp., and *Cosmarium* sp. collected from Kenfig Pool near Bridgend (Pl. 6, figs. 1, 2).

The zoosporangia were spherical or subspherical and 6–8μ in diameter, at maturity containing 4–6 zoospores. There was no discernible discharge papilla. On release of the zoospores the thin wall of the zoosporangium collapsed. The zoospores were spherical and 3–3·5μ diameter with a single eccentric hyaline oil globule 0·5–1μ diameter. The rhizoidal system consisted of a single delicate main rhizoid which branched once or twice only. The resting spore was not seen.

Rhizophydium mammillatum (Braun) Fischer

This organism occurred as a weak parasite or saprophyte on cells of *Cladophora* collected from a ditch in a railway cutting (Coity branch line), near Bridgend, Glamorgan (Pl. 6, figs. 3–5).

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The zoosporangium was sessile on the host cell wall and varied in shape from ovate to broadly pyriform and citriform, but was chiefly shortly ovate. The specimens of zoosporangia observed were between $12 \times 10\mu$ and $17{\cdot}5 \times 14\mu$ in size. The apex of the zoosporangium was usually produced into a fairly prominent papilla, the tip of which dissolved to form the escape pore. Inside the host cell the chytrid consisted of a slender main rhizoid which bore a few delicate branches. The zoospores were $3–4\mu$ in diameter, globose, with a laterally placed hyaline globule about $1–2\mu$ in diameter.

Though the resting spores are so far unknown, in this material some structures were produced which may have been resting spores. They closely resembled the zoosporangia in size, shape and development and ultimately contained a mass of globules (as in the zoosporangium in Pl. 6, fig. 4) which became brownish yellow tinted. No further development was observed in these structures.

Entophlyctis confervae-glomeratae (Cienkowski) Sparrow

This species was found living in cells of filaments of *Oedogonium* and *Spirogyra* brought from a pond in a disused cement works near Primrose Hill, Llandaff, Cardiff (Pl. 6, fig. 6).

The intramatrical zoosporangia were spherical to subspherical in shape and varied from $10{\cdot}5 \times 10$ to $7 \times 6\mu$ (usually $9 \times 8\mu$) in size, with one, sometimes two, main rhizoids at the base and a single apical escape tube at maturity. The zoospores were $4–4{\cdot}5\mu$ in diameter, spherical to ellipsoidal with an eccentric oil globule about 1μ in diameter. After release by the deliquescence of the tip of the discharge tube, they remained clustered for a short time at the mouth of the escape tube before darting away. On emptying, the zoosporangium became wrinkled and collapsed owing to its very thin wall. The escape tube varied from 4 to 9μ in length and 2 to $2{\cdot}5\mu$ in diameter, tubular in shape and broadening at its insertion on the zoosporangium. The rhizoids bore frequent fine branches which tapered gradually to their very fine tips and extended up to 80μ from the zoosporangium.

Some thalli grew to produce reproductive bodies which were borne like the ordinary zoosporangia and resembled them in size and shape, but had a relatively thick, usually two-layered wall, coloured a pale brownish yellow. When, after several days, some of these bodies produced zoospores in the same manner as the normal thin-walled zoosporangia, the thick wall of this body retained its shape and smooth outlines, and did not wrinkle as did the thin-walled zoosporangia. These thicker-walled bodies had every appearance of resting spores. However, if these bodies are resting spores this method of germination is very different from the only two other records of germination of resting spores in *Entophlyctis*. Fisch reported that in the resting spores of *E. vaucheriae* water was taken in and the contents swelled, bursting the exospore. The contents became extruded within the endospore, and within the vesicle so formed the zoospores were produced (Sparrow, 1943, p. 251). In *E. aurea* (Haskins, 1946) the resting spore behaves as a prosporangium. However, *E. aurea* shows greater affinities

with *Karlingia* than it does with the other species of *Entophlyctis*. Karling (1947) believed it to be *Karlingia rosea* (De Bary & Woronin) Johansen.

Entophlyctis confervae-glomeratae was never found inhabiting healthy looking cells but only pale or discoloured cells. However, the chytrid would not infect any boiled plant fragments, including filaments of *Spirogyra* and *Oedogonium*, which were placed in unifungal cultures of the chytrid. Karling (1931*a*), reported similar results with *Entophlyctis helioformis* (Dang.) Ramsbottom.

This species has also been recorded by Sparrow (1936) as *E. cienkowskiana* on *Cladophora* sp. from the Cambridge district (see Canter, 1953).

Entophlyctis bulligera (Zopf) Fischer

This species occurred in cells of *Spirogyra* filaments brought from Kenfig Pool, near Bridgend, Glamorgan.

The intramatrical zoosporangia were spherical, 13–16μ diameter with an epibiotic 'knob'—the zoospore cyst—measuring 3·5–4μ diameter. To the underside of the zoosporangium were attached one to two main rhizoids which were fairly coarse, 1–2μ wide and extending, with frequent branchings through several host cells often on both sides of the zoosporangium. The resting spore was not observed.

Cladochytrium replicatum Karling

This organism appears to be widespread in nature and has been found in plant debris brought from Pysgodlyn Mawr, St Donat's; Llyn Fach, Craig y Llyn, Hirwaun; and the lake at Glyn Cornel, Llwynypia (Pl. 7, figs. 1–4).

The zoosporangia borne on lateral branches of the thallus were mainly spherical, sometimes ovoid, and occasionally irregular when they were confined by the host cell. They measured 14–18μ in diameter, most frequently 17–18μ and usually bore a single exit tube, sometimes two, which was 8–16μ in length and about 2μ wide, frequently somewhat curved and usually reaching to the outside of the host cell. The zoospores were about 6μ in diameter with an eccentric golden-brown refringent oil globule 1–2μ in diameter of a highly plastic consistency, frequently appearing oval-shaped, spherical, indented, and comma-shaped. On release they formed a temporary motionless mass at the mouth of the escape tube before becoming active and swimming away. Resting spores were not observed in this material.

C. replicatum has also been recorded by Sparrow (1936) occurring on leaves of Elodea and decayed grass leaves from aquatic sites at Wicken, Cambridge and Surrey.

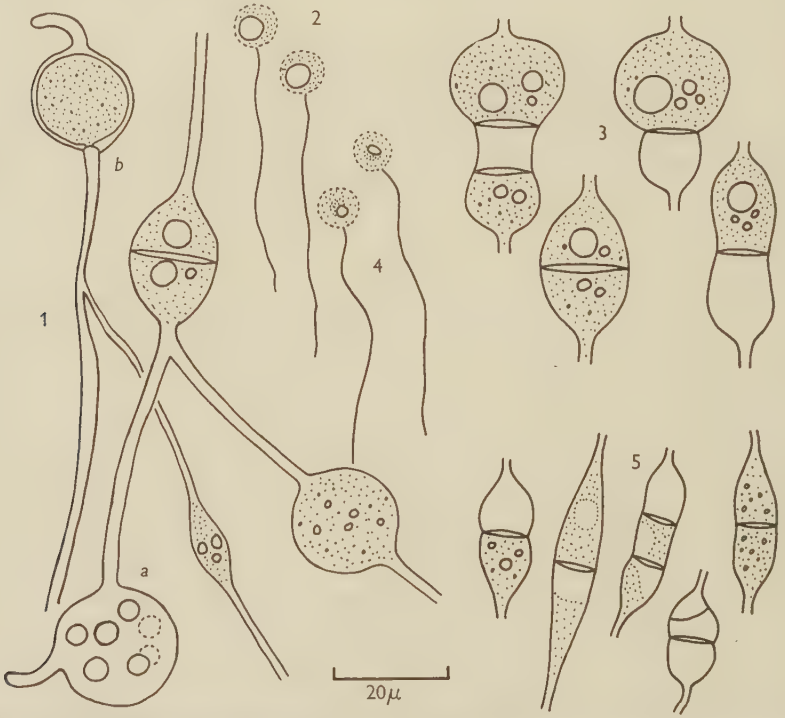
Cladochytrium aurantiacum sp.nov.

This species was found in fragments of leaves, stems and roots of *Avena* and *Triticum*, which had been staked out in the Glamorgan Canal, Cardiff. It resembles *C. replicatum*, but is somewhat larger in most respects. Many

individuals of three or four generations were observed in unifungal culture and as this species differed in several features from each of the known species of *Cladochytrium* it is diagnosed here as a new species.

Cladochytrium aurantiacum sp.nov. (Text-figs. 1–3)

Thallus polycentricus, intramatricalis. Zoosporangia inoperculata terminalia in ramis lateralibus, maxime sphaerica ad subsphaerica 18–24 μ (saepe circ. 22 μ) diam., proliferantia. Cytoplasma hyalina, globulis aurantiacis refractis in maturitate. Membrana terres tenuis sine colore. Rhizoidea tubulata circ. 2 μ diam., extenta sed ferentia pauca tubera irregularia solum. Amplificationes comparate rarae, magnae, ovatae vel paene globosae 10–20 μ diam., globulis hyalinis oleariis et 0–3 septa. Zoosporae sphaericae 6–7 μ diam., uno eccentrico magno sphaerico aurantiaco globulo diam. 3·75–4·25 μ., et ferentes flagellum longum posterius. Spora perdurantis non visa. Saprophyticum in fragmentis foliorum cerialium.



Text-fig. 1. *Cladochytrium aurantiacum.* Portion of the rhizomycelium bearing a zoosporangium (*a*), proliferating zoosporangium (*b*) and spindle organs.
Text-fig. 2. *C. aurantiacum.* Zoospores.
Text-fig. 3. *C. aurantiacum.* Typical spindle organs.
Text-fig. 4. *C. replicatum* (for comparison). Zoospores.
Text-fig. 5. *C. replicatum* (for comparison). Typical spindle organs.
(Drawn with the aid of Watson camera lucida. ×775.)

The zoosporangia (Text-fig. 1 *a*) are mainly spherical to subspherical 18–24 μ in diameter (usually about 22 μ), but irregularly shaped zoosporangia occur in narrow host cells. They bear narrow discharge tubes

8–12 μ long (Text-fig. 2 *b*). The young zoosporangium is hyaline, but as it matures the globules in the cytoplasm become reddish-golden or orange in colour. The zoospores are spherical, 6–7 μ diameter with an eccentric large spherical orange globule 3·75–4·25 μ diameter and a long posterior flagellum (Text-fig. 2). They are released by the deliquescence of the tip of the escape tube and remain for a few minutes in a motionless cluster outside the escape pore before becoming active and swimming away. Secondary zoosporangia are also produced as in *C. replicatum* by the proliferation of the subtending rhizoidal branches into the empty primary zoosporangium Text-fig. 1 *b*). The tubular rhizoids are profuse, and broader than in *C. replicatum*, being usually about 2 μ wide, with few irregular swellings. The spindle organs (Text-fig. 4) resemble those of *C. replicatum* in structure but occur only infrequently along the rhizoidal branches, and are larger, as can be seen by comparing Text-figs. 3 and 5. The oil globules accumulated in the spindle organs of the new species of *Cladochytrium* are hyaline and have not been observed to become coloured as in the spindle organs of *C. replicatum*. Resting spores have not been observed.

Germination of the zoospores, development of the thallus, and growth and development of the zoosporangia are identical with those same stages in *C. replicatum* so fully described by Karling (1931 *b*, 1935).

Only two other species of *Cladochytrium* produce zoospores with golden coloured globules—*C. replicatum* and *C. aureum* Karling (1949). The new species differs from these in its larger rhizoids, spindle organs and (generally) zoospores. The spindle organs are fewer and remain hyaline in the new species while being numerous and becoming coloured with the golden globules in the others. The zoosporangia of *C. aureum* lack exit tubes. The globule in the zoospore in *C. aurentiaca* is larger and even more striking than in the other two species.

The remaining four known aquatic species of *Cladochytrium*—namely *C. tenue* Nowakowski (Sparrow, 1943, p. 309), *C. hyalinum* Berdan (1941), *C. crassum* Hillegas (1941), and *C. setigerum* Karling (1951)—as well as differing from the new species in several other characters, are hyaline throughout their life cycle.

I am grateful to Prof. R. C. McLean and the late Dr W. R. Ivimey-Cook for much encouragement and guidance, and to Dr R. H. Haskins for reading the manuscript.

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EXPLANATION OF PLATES 6 AND 7

Plate 6 (×600. Original negative, ×180.)

Figs. 1, 2. *Rhizophydium Constantineani*. Fig. 1. Very young and old thalli on *Oedogonium* sp. Fig. 2. Mature thallus on *Cosmarium* sp.

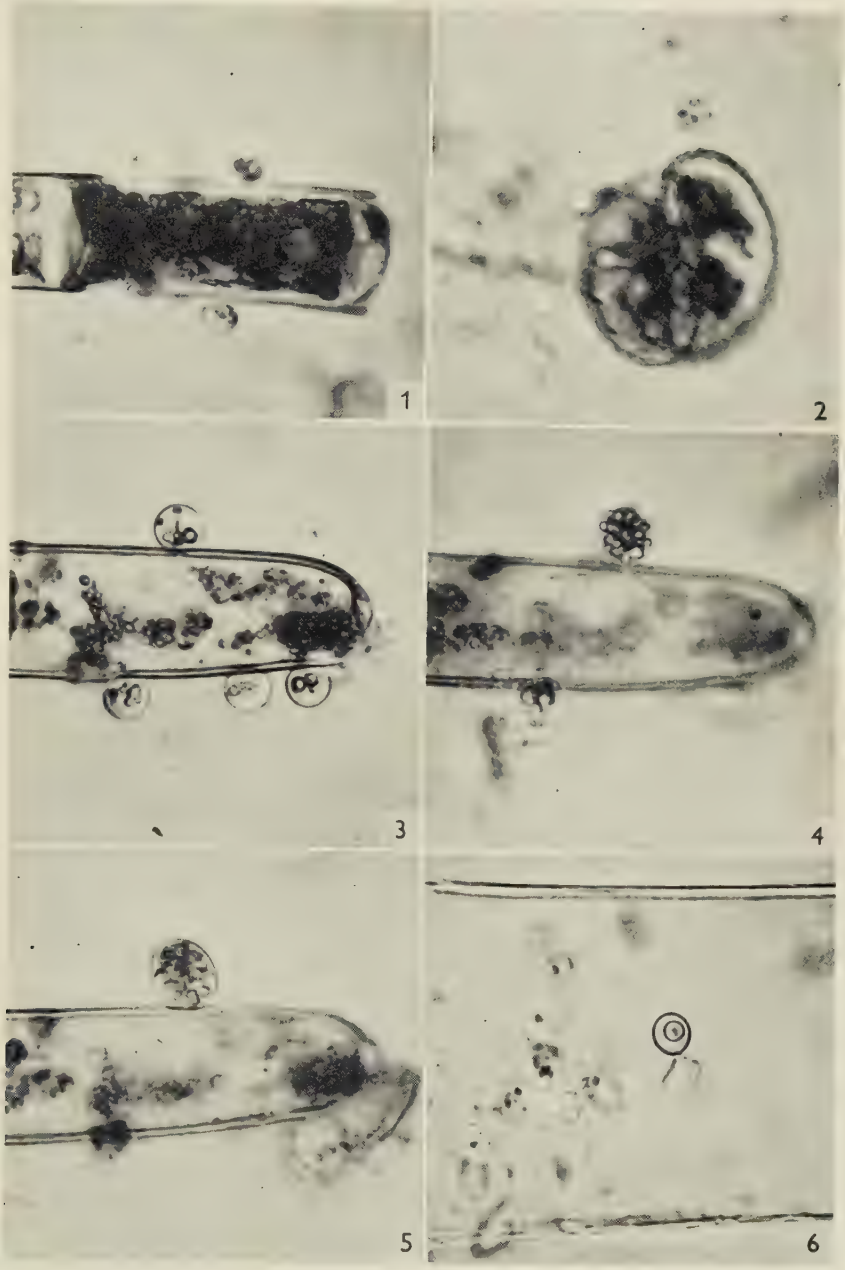
Figs. 3–5. *Rhizophydium mammillatum* on *Oedogonium* sp. Fig. 3. Young thalli. Figs. 4, 5. Same thalli mature.

Fig. 6. *Entophlyctis confervae-glomeratae* in a cell of *Spirogyra* sp.

Plate 7 (×600. Original negative ×180.)

Figs. 1–4. *Cladochytrium replicatum*. Fig. 1. Rhizomycelium bearing spindle organs in fragment of *Avena* leaf. Figs. 2, 3. Normal mature zoosporangia. Fig. 4. Giant zoosporangium almost filling host cell.

(*Accepted for publication* 11 *July* 1955)



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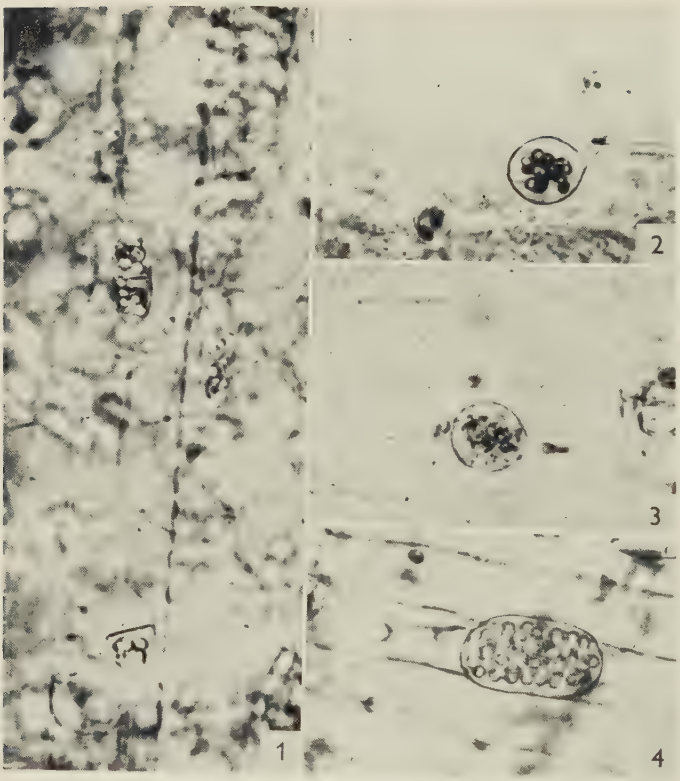
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Trans. Brit. mycol. Soc. **39** (2), 267–277 (1956).

AN OAK (*QUERCUS ROBUR* L.) CANKER CAUSED BY *STEREUM RUGOSUM* (PERS.) FR.

By SACHINDRANATH BANERJEE

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(With Plates 8 and 9, and 1 Text-figure)

A hitherto unreported destructive oak canker in Scotland and its causal organism, *Stereum rugosum*, have been studied and described from Dawyck, Peebleshire. The cankers, which have been found on trunks of trees about 50–60 years old growing in a damp and shady situation, are mostly open with a depressed to hollow centre which is surrounded by a prominent callus ridge and are often laterally extended. The fructifications of *S. rugosum* have been found at the edge or near the centre on the surface of the dead bark, usually around the stub of a dead branch.

Microscopic characters of the rot are fully described and chemical changes in the wood during the process of decay have been examined.

S. rugosum has been obtained in pure culture from areas of both advanced and incipient decay and also from spores. It can be easily identified in culture by its characteristic dense, white, cotton-woolly to felty mycelium, rapid growth and distinctive buff or pinkish buff colour of the mat with age.

Inoculations, made on the wounded bark on the trunk of healthy oak tree employing mycelium as the inoculum, were positive.

Laboratory studies showed *S. rugosum* to be able to attack sapwood much more readily than heartwood.

Introduction

Stereum rugosum (Pers.) Fr., known to cause a white pipe rot of oak (*Quercus robur* L.), has been regarded as a fungus of minor importance on standing trees in Great Britain (Cartwright & Findlay, 1938, 1946). Recently, attention of the writer was directed to a destructive canker of oak in a private plantation (Balfour Estate) at Dawyck, south-west of Edinburgh, Scotland. After close examination of the diseased trees fructifications of a fungus were found on or near the cankered areas and the fungus was identified as *S. rugosum*. Further investigations showed that *S. rugosum* was responsible for the cankers. The affected trees were about 50–60 years old and growing in a mixed stand with larch, sycamore and beech. For the most part the oak trees appeared to be in good condition, but about a dozen of them showed cankers on their trunks. The infected trees looked unhealthy, their tops were poor and they were in the process of dying. The situation was rather damp and heavily shaded; the soil dampness and relatively high humidity of the air were suitable for such a fungal infection.

Although the causal organism has been known to occur in Great Britain for about 100 years or more, its activity as a canker-forming parasite on oak is not appreciated in this country. A somewhat similar

canker caused by a species of *Stereum* was described by Potter (1901) from the north of England, and he named the fungus as *S. quercinum*. Such canker-formation is, however, known to occur on the continent of Europe. Eddelbuttel (1911) described canker-like wounds with fructifications of *S. rugosum* on a young oak and on an apple tree; these cankers resembled those on larch in outward appearance. Rea (1922) considered *S. quercinum* Potter to be synonymous with *S. spadiceum* Fr. (syn. *S. gausapatum* Fr.) which causes a heart rot of oaks in North America (Davidson, 1934) and a pipe rot of oaks in Britain. Liese (1930) first suggested that Potter's fungus was *S. rugosum* when he described a canker of the oak associated with *S. rugosum* in a private wood near Berlin, and a similar view, which the results of the present investigation endorse, was held by Bergenthal (1933–34) who observed oak cankers at various places in Germany and found *S. rugosum* always to be the cause of the disease. Similar cankers have been reported from Denmark by Ferdinandsen and Jorgensen (1938–9).

The aim of this study was to describe and illustrate the canker disease and its causal organism. It was also necessary to determine, by means of artificial inoculation experiments in the field, the parasitic activity of the fungus and the damage it causes to oak wood under controlled conditions.

Symptoms

The cankers on the living trees were somewhat oval but most often elongated with depressed centres and swollen margins and were associated with decay (Pl. 8, fig. 2). There was considerable distortion of the trunk which rendered them conspicuous, especially when more than one canker occurred on the same trunk. Cankers, measuring 16–34 × 12–14 in., were found at heights of 1–6 ft. or more upwards from the base. Sometimes two cankers were found, one above the other, on opposite sides of the stem (Pl. 8, fig. 1). Near the cankered area the trunk usually bulged out, and there was localized flattening of the stem on one side. In a comparatively young canker the remnant of the stub of a dead branch could be seen at the centre (Pl. 8, fig. 2). Numerous fructifications of *S. rugosum* developed either near the margin or on the central portion of the cankered areas, usually around the stub of the dead branch (Pl. , fig. 2). In an advanced stage of decay a cavity surrounded by a prominent callus ridge was formed; its edge often bulged out owing to lateral extension. Eventually, a gaping wound surrounded by a raised callus-tissue developed and never healed. In extreme cases of decay, both sapwood and heartwood became discoloured, light, soft, somewhat spongy, and ultimately becoming brittle crumbled readily into flakes or powder on drying. Sometimes the sapwood separated along the annual rings and sheets of whitish mycelium was found in between these cracks and between the bark and the sapwood. Sections from such extreme decay showed that the summerwood was mostly a network of middle lamellae, and it was in this region of the annual ring that separation occurred. A cross-section through a canker (Pl. 8, fig. 5) showed that the decay extended into the heartwood which was

completely exposed, the sapwood being completely decayed. In other cases, the sapwood was found to be badly decayed. The progress of decay in the heartwood was comparatively low. A narrow dark-brown invasion zone of the rotted heartwood was always visible towards the exposed surface of the canker. Tissues outside this zone appeared perfectly sound. Lateral extension at the edge of the canker to heal the wound was clearly visible. After the formation of the canker no complete annual ring was formed. The wood in the upper and the lower regions of the cankered stem, however, appeared normal.

THE SPOROPHORE OF *STEREUM RUGOSUM* (PERS.) FR.

Usually resupinate and stretched out flat on the substratum, sometimes effuso-reflexed with a narrow, free, upturned marginal pileus (Pl. , fig. 3), diameter of the resupinate portion 1–6 cm., reflexed portion about 2–10 mm. deep and 0·5–2 mm. thick; often laterally confluent with the reflexed portion imbricate; leathery to corky, becoming hard on drying; margin thick, entire, often obtuse, pale coloured. *Upper Surface.* At first silky and Pinkish Buff (Ridgway, 1912) in colour; becoming glabrous and concentrically zoned with age; radially furrowed; Pinkish Buff towards the margin but drab grey to Vinaceous Drab on weathering. *Context.* Thin; coriaceous to rigid; whitish to yellowish. *Hymenial Surface.* Pruinose, dull; bleeding red when fresh if cut or bruised; sometimes uneven; pale Pinkish Buff to Pinkish Buff, often becoming greyish with age. *Basidia.* Elongated, clavate; dimension about 38–50 × 5–6 (7·5) μ. *Spores.* Hyaline; smooth, oblong and somewhat flat at one side, often slightly curved; dimension about 8–12 × 3–4·5 μ. *Cystidia.* None. *Lactiferous Cells.* Numerous, curving up into the hymenium from the underlying tissue; slightly flexuous; reddish brown in colour; about 3–6 μ in diameter. *Tissue Differentiation.* The fructifications are about 600–1600 (2000) μ thick, and the following regions can be differentiated: (*a*) a hymenial layer, 2 to many zoned, about 100–700 (1300) μ thick (Pl. 8, fig. 4); (*b*) an intermediate layer, about 300–500 μ thick, and consisting of thick-walled, hyaline, closely septate, parallel hyphae, about 2·5–3 μ wide, mostly empty; (*c*) a golden-yellow zone, about 80–100 μ thick lying between the intermediate layer and the outermost hairy covering, composed of longitudinally arranged hyphae; and (*d*) the hairy covering, about 100–400 μ thick, consisting of hyaline or pale coloured, straight or slightly flexuous, septate hyphae, about 2·5–4 μ wide, often matted.

The above description has been based on material collected in January and July 1950 at Dawyck.

In Great Britain, the fructifications of *S. rugosum* are commonly found on stumps, trunks and fallen branches of broad-leaved trees. The bleeding hymenium and the presence of dark-coloured conducting organs place this fungus near *S. sanguinoleutum* and *S. gausapatum.* It can be readily distinguished from them by its characteristic multizonate hymenium (Pl. 8, fig. 4) and more woody texture.

Decay of Oak

Microscopic details of the rot

In order to determine the extent of damage caused by the fungus within the host tissue, small pieces of sound and infected wood in various states of decay were sectioned both free-hand and with the microtome. Transverse, radial and tangential sections of the wood, about 15–20 μ thick, were cut only after softening the materials by immersing the blocks in gently boiling water until they became water-logged and sank. As it was very difficult to observe hyphae in the sections of the heartwood in an incipient stage of decay, differential staining was undertaken with safranin and picro-aniline-blue as described by Cartwright (1929) with satisfactory results.

In an incipient stage of decay the mycelium is rather scanty, but as the decay advances, hyphae becomes distributed throughout all the elements of the heartwood, being particularly plentiful in the vessels, medullary rays and wood parenchyma (Pl. 8, figs. 7, 8). The hyphae, sometimes filling entire cavities of the fibres, wood-parenchyma and ray cells and forming compact masses, are rather fine, profusely branched, usually hyaline, occasionally yellowish brown, about 1–3 μ in diameter and with infrequent clamp-connexions. The hyphae within the fibres and tracheids are often seen to run in a more or less longitudinal direction. A gradual thinning out of the secondary walls of the fibres from the lumen towards the middle lamellae is evident, but less commonly in the tracheids. The vessels, wood-parenchyma are least affected, although the tyloses are often broken down (Pl. 8, fig. 6). The wood parenchyma cells scattered among the fibres and tracheids show little evidence of decay, excepting the presence of numerous bore-holes through which the hyphae pass. The hyphae at first ramify through the pits, but later pierce the cell-walls. The resulting bore-holes, which are abundant in an advanced stage, are at first circular, but later more or less elongated and about 1–4 μ across. Dark coloured, brown to blackish gummy materials are present in the parenchyma and ray cells. In case of extreme decay the wood presents the appearance of a network of middle lamellae but the vessels, rays and wood parenchyma are still recognizable. The elements break apart easily and can be teased out for examination. On being treated with phloroglucin and hydrochloric acid they turn pink which indicates that some amount of lignin is still present.

Microchemical studies

Tests for cellulose and lignin in the normal and partly decayed heartwood were made by staining the sections with chlor-zinc-iodine for cellulose and phloroglucin and hydrochloric acid for lignin. The results are summarized in Table 1 from which it will be evident that the fungus can gradually digest both cellulose and lignin during the process of decay, the heavily lignified parts being partially affected. Fahraeus, Nilson & Nilson (1949), while studying the decomposition of wood by some white rot fungi, have shown that *S. rugosum* utilizes cellulose in preference to lignin. In oak the tyloses are lignified structures and give positive lignin reaction. Sometimes the faint blue colour with chlor-zinc-iodine may

possibly be explained as due to the presence of a thin secondary wall of cellulosic material which responds to the test. Although broken down at places, they are present in an advanced stage of decay being filled with hyphae and perforations in their walls but these usually fall apart during the process of sectioning.

Table 1. *Results of staining for cellulose and lignin in normal and partially decayed heartwood of oak* (Quercus robur) *with chlor-zinc-iodine and phloroglucin-HCl*, respectively

Elements	Normal heartwood	Decayed heartwood
	Cellulose (Chlor-zinc-iodine)	
Vessels	Tyloses faint blue to sometimes colourless	Tyloses broken down in places; remnants faint blue to colourless
Fibres	Secondary walls mostly faint blue, often colourless	Secondary walls light blue to colourless, particularly near the lumen; sometimes entirely light blue and often blue at places
Tracheids	Secondary walls in some cases light blue	Secondary walls sometimes faint blue to almost colourless
Wood parenchyma	End-walls at times blue	Secondary walls sometimes light to faint blue; end walls often colourless
Ray cells	Some secondary walls light blue	Secondary walls often light blue or lavender
	Lignin (phloroglucin-HCl)	
Vessels	Tyloses red to colourless; primary and secondary walls deep red	Tyloses pale pink to colourless; primary and secondary walls red to light red
Fibres	Primary walls red; secondary walls light red to pink, often colourless	Primary walls light red to pink; secondary walls mostly pink to colourless
Tracheids	Primary walls red; secondary walls red near middle lamella, pink to colourless near the lumen	Primary walls red to light red; secondary walls mostly pink to colourless
Wood parenchyma	Primary walls red; secondary walls light red	Primary walls light red; secondary walls pale pink
Ray cells	Mostly red	Primary walls red to light red; secondary walls mostly pink, sometimes colourless

Decay resistance tests

In order to determine under controlled conditions the natural resistance of oak samples to decay by *S. rugosum*, woodblock cultures of the fungus were made in 500 ml. Erlenmeyer flasks, each containing 250 ml. of 2·5 % malt agar which was slanted after sterilization. The flasks were inoculated with actively growing mycelium and incubated at 23° C. in darkness. Within a week the mycelium nearly covered the surface of each slant and was ready to receive the test-pieces.

The test-blocks (0·5 × 0·5 × 2·0 in.) were cut from sound wood, with the long axis parallel to the grain, and serially numbered. The heartwood and sapwood blocks were tested separately. To determine the loss due to decay the blocks were dried at 60° C. to constant weight. The blocks were

put into Roux tubes, each having distilled water at the bottom and sterilized by autoclaving at 15 lb. for 10 min. This method of sterilizing kept the atmosphere around the blocks more or less saturated during the process so that little loss of water could take place from the wood blocks, and consequently a shorter time was required for sterilization as pointed out by Chidester (1937, 1939). The test-pieces were then placed individually on cultures and then kept at 23° C. in darkness for 4 months. After the completion of the test, the blocks were taken out of the flasks, the superficial mycelium was carefully removed without damaging the wood blocks, weighed and again dried to a constant weight. The percentage losses, based on the dry weight of the sound material, were calculated. The average moisture-content of another set of sapwood and heartwood blocks before and after they were exposed to fungal action were determined in the same way. This was necessary to determine whether the moisture-content of the wood-blocks was much above the fibre-saturation-point or not during the test period as this was essential for the satisfactory growth of the fungus. The average moisture-contents of the heartwood and the sapwood, after sterilization, were found to be 55·5 and 90·2 %, respectively. No attempt was made to control the moisture content after they were exposed to fungal action in order to establish its relation with the progress of decay.

Within a month after inoculation all the faces of the sapwood blocks were completely covered with vigorously growing dense, uniform, cotton-woolly mycelium which later became felty (Pl. 9, fig. 4). The mycelium was mostly white but Light Buff colour appeared in patches with the age of the culture. On heartwood blocks, on the other hand, even after a month the growth was rather poor, thin, cotton-woolly and patchy, becoming somewhat felty at places (Pl. 9, fig. 3).

The results of the experiment are summarized in Table 2 which shows that the difference between mean loss per cent. in sapwood and heartwood is 4·62, and that this is highly significant. The sapwood and the heartwood may be classed under Findlay's (1938) 'non-resistant' and 'moderately resistant' groups, respectively, with respect to *S. rugosum*.

Table 2. *t-test of the difference between mean loss percentage of sapwood and heartwood of oak*

	Replicates	Mean loss (%)	Standard error of mean	Difference between mean loss in sapwood and heartwood	*t*	Probability
Sapwood	12	10·83	±0·36	4·62	12·56	<0·001
Heartwood	12	6·21	±0·09			

The average moisture-contents of the sapwood and heartwood blocks after completion of the test rose to 131·3 and 83 %, respectively; due to absorption of water from the agar medium.

Culture studies

S. rugosum was grown in culture and its characteristics studied on potato-dextrose agar and 2·5 % malt agar. The pH value of each medium was adjusted, and after sterilization was found to be 5·2. The initial cultures were made by the use of spores from fresh sporophores found on the surface of oak cankers and from portions of the decayed heartwood. Cultures from diseased tissues were obtained from the areas designated by the numbers 1, 2 and 3, while from areas 4 and 5 no cultures could be secured (Text-fig. 1). Microscopic examinations of the sections taken from these regions showed that hyphae were not present in 4 and 5. The hyphae could not, therefore, penetrate far beyond the invaded zone. After careful

Text-fig. 1. Diagrammatic T.S. of oak canker (see text).

comparison it was found that the cultures obtained from the infected wood were identical with the polysporous ones in both cultural and microscopic details.

The colour exhibited by the mycelium during growth has been expressed according to Ridgway (1912) and the terms used to describe the texture of the mat are those of Long & Harsch (1918).

Oxidase tests

Bavendamm's test (1928) for detecting the presence of oxidases characteristic of the white rot fungi showed *S. rugosum* to be capable of decomposing lignin with other substances. The intensity of reaction was, however, at first mild on gallic acid medium, but later it became intense. The diameters of the rings after 48 and 72 hr. were 12 and 15 mm., respectively. The fungus also gave a positive reaction to the test recommended by Preston & McLennan (1948), and partially bleached the colour of gentian violet present in the medium, but about 6 weeks' incubation was necessary before definite results could be obtained.

Cultural characteristics

(1) *Habit.* On *potato-dextrose agar* at 18° C. the growth started rapidly, and within 2 days after inoculation thin cottony mycelium appeared over the inoculum, together with an appressed and sodden growth, about 3–4 mm. across, over the surface of the slant. Condensation of the mat started early, and in about 5–6 days the inoculum turned felty, but the mat proper became differentiated into a broad cotton-woolly zone, about

5–6 mm. wide and an appressed, colourless zone of advance. As growth proceeded, there was a felty ball over the transplant, and the whole surface of the slant covered in about a week with a smooth, soft, homogeneous, felty mat. After a month the surface of the mat became uneven due to the formation of small, raised and felty areas. The medium was discoloured and became pale yellow in cultures, 10 days old. No marked difference in cultural characteristics was shown by cultures grown at 23° C, except that there was early condensation of the mycelium to form a smooth, even and felty mat. On *malt agar*, on the other hand, at 18° C. the growth was poorer than that on potato-dextrose agar. There was little aerial mycelium and its condensation was somewhat delayed. It was for the most part thin and cotton-woolly with an indistinct and narrow advancing zone while the inoculum was subfelty. In about 10 days the lower half of the slant tended to become felty and towards the end of third week became entirely so. The medium became somewhat pinkish in cultures, 10 days old. At 23° C., the growth was more or less the same as that at 18° C., but aerial mycelium was formed and part of it became cottony within 5 days after inoculation.

(2) *Colour.* On *potato-dextrose agar*, coloration appeared at about 5 days after inoculation over the transplant as a patch of Light Buff or Salmon Buff. The central portion of the mat turned Pinkish Buff in cultures, 10 days old, other portions remaining white till the end of the fourth week when Light Buff appeared on the lower half of the mat around the inoculum. At 23° C. the pigmentation of the mat was more or less the same but patches of Light Buff appeared over the white mat in cultures 35 days old. On *malt agar*, on the other hand, coloration at both temperatures first appeared after a fortnight, only over the transplant as a patch of Warm Buff. Later, Light Buff and pale Antimony Yellow appeared throughout the whole mat in both cases, but it seemed to be more pronounced in cultures kept at 18° C.

(3) *Rate of growth.* (Pl. 9, figs. 1, 2). The rate of growth, both on potato-dextrose agar and malt agar kept under identical conditions, was more or less the same, the daily increment in growth being 10·5 mm.

(4) *Hyphal characters. Aerial mycelium*—two types of hyphae could be recognized: (*a*) thin-walled, hyaline hyphae, about 3–4 μ in diameter, comparatively few more or less straight, distantly branched and septate, with occasional simple clamp-connexions, H-connexions frequent; and (*b*) thin-walled, hyaline hyphae, about 1–2·5 μ in diameter, numerous, much branched, branches originating usually at right angles to the main hypha, distantly septate, straight or flexuous, often spirally coiled, clamp-connexions rare.

Submerged mycelium—the same two types of hyphae could be recognized, but with slight differences, viz. (*a*) wider hyaline hyphae more frequent, about 4–5 (6) μ wide, much branched, septate closely or infrequently, straight or flexuous, with coarsely granular contents, often sparse, clamp-connexions rare; and (*b*) finer, much branched, flexuous hyphae, about 1·5–3 μ wide, with coarse granular contents, hyaline or with a yellowish tint, clamp-connexions rare, originating from the wider hyphae and often clustered.

Production of fruit-bodies in culture

Cultures of *S. rugosum* on various media in test-tubes did not form fructifications. However, while making decay resistance tests with oak samples in Erlenmeyer flasks, small resupinate fructifications appeared on the surface of the malt agar slant near the bare glass surface in cultures about 4 months old. The medium for developing sporophores recommended by Badcock (1941) was then tried. Beech and spruce sawdust, mixed separately with Badcock's 'accelerator' in varying proportions (5–40 % by weight), after being soaked in water, were used in Petri dishes, test-tubes (20 × 4 cm.) and Badcock's apparatus (Badcock, 1943). After sterilization the media were inoculated and the cultures kept in darkness at room temperature (18–21° C.) inside a closed chamber in which a moderately high humidity was maintained. Subsequently, when the mycelium entirely covered the surface of the medium or permeated through the medium within the tubes, all cultures were removed and placed in strong diffused light on a table about 8 ft. from a large window of the laboratory. The fungus made exceptionally rapid and luxuriant growth on the sawdust medium, particularly on those containing 30–40 % by weight of the 'accelerator'.

It was only in Petri-dish cultures with 30–40 % 'accelerator' that the mycelium began to form small, fertile, resupinate fructifications, sometimes with a narrow, marginal, hairy pileus near the rim of the Petri dish in about 3–4 months after inoculation. The upper surface was somewhat greyish, but the hymenial surface was Light Buff in colour. In test-tubes the fruit-bodies were not formed, although there was much condensation of the superficial mycelium near the opened mouth of the tube. In Badcock's apparatus, on the other hand, irregular resupinate growths which did not develop further were noticed outside the rim of the test-tubes within the flask, after 5–6 months.

Field inoculations

During the summer of 1950, two inoculations were made on the trunk of healthy *Quercus robur*, about 20-year-old, located in a private plantation at Dawyck. Small pieces of agar with actively growing mycelium from cultures were introduced into a wound made by making a cross incision, about 2 × 2 in., through the bark so as to obtain a flap of the bark still attached to the trunk. Before making the incision the surface of the bark was wiped over with absolute alcohol and then with sterile distilled water in order to remove the surface contaminations as far as practicable. Equal numbers of controls were also established. After putting the inoculum under the flap, the wounds were protected by a piece of moist sterile cotton-wool above each incision and covering the whole with thick brown paper tied with a string. These were, however, later removed and both series left exposed.

After 4 months the wound inoculations were found uniformly positive (Pl. 9, figs. 6, 7) while the controls remained flat and healed up. The

surface of the bark around the infected regions was swollen, somewhat soft, slightly discoloured and each wound was hollow and gaping open at the centre. The callus tissue was not formed, and this apparently showed that within a short time sufficient mycelium had been produced to parasitize the living bark and the underlying tissues.

In March 1951, they were again examined and the inoculated portions were removed. A cavity about 1 in. wide, 2 in. long and half an inch deep had been formed (Pl. 9, figs. 7, 8). The spread of the mycelium was limited by a narrow, brown, rotted zone in the sapwood. Mycelium has been observed in all the elements of the sapwood. Re-isolations from the infected tissues were subsequently made and these agreed with the original cultures of *S. rugosum* in all essential details.

Control measures

No certain method of cure for severely cankered trees can be suggested. In order to reduce the danger of spread to other oak trees, the cankered trees should be removed from the plantation; this will make openings in the crown cover and thereby alter the density of the plantation and humidity of the situation. The affected and dead branches should be covered with a paint in order to protect the surface from moisture. An alternative method is to apply a fungicide to the cut surface. As both vigorous and non-vigorous trees are susceptible to the disease under unsuitable conditions, thinning would be advisable in order to admit more light and ventilation into the plantation.

This investigation has been carried out under the supervision of Dr Malcolm Wilson, formerly Reader in Mycology, University of Edinburgh. I take this opportunity of expressing my indebtedness and deep sense of gratitude for his guidance and helpful criticisms. My grateful thanks are due to Prof. Sir William Wright Smith, F.R.S. for his kindness in offering me facilities to work in the Mycology Laboratory, Department of Botany, University of Edinburgh. I also record with pleasure my appreciative thanks to Mr Balfour, owner of the Estate at Dawyck, for the materials furnished and for allowing me to carry out experiments in the field.

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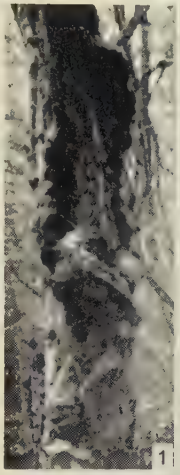

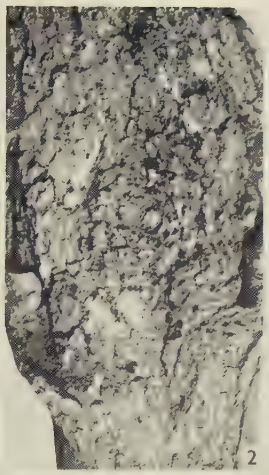

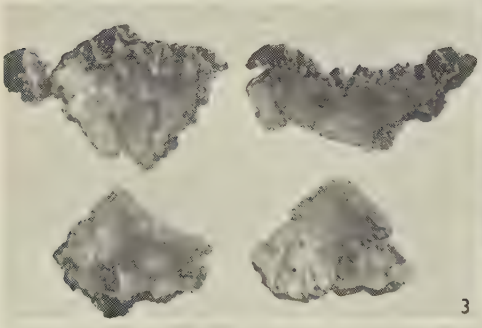

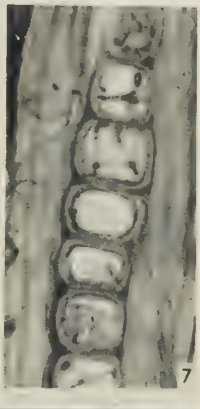

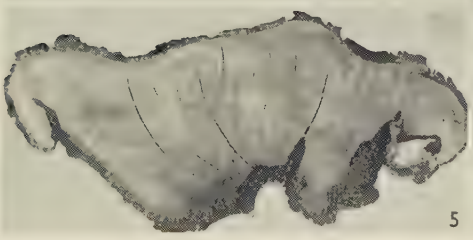

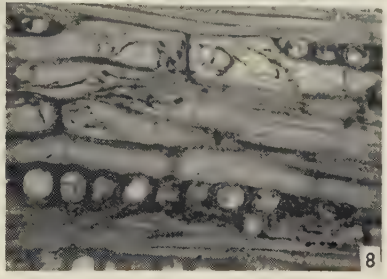

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(*Accepted for publication* 31 *July* 1955)

EXPLANATION OF PLATES

Plate 8

Fig. 1. General appearance of a heavily cankered oak (*Q. robur*); two cankers are seen situated one above the other.
Fig. 2. A comparatively young canker showing characteristic swelling and flattening of one side of the trunk; resupinate fructifications of *Stereum rugosum* can be seen on the decaying bark around the rotten branch stub at the centre.
Fig. 3. Effuso-reflexed fructifications of *S. rugosum* found growing near the margin of the canker.
Fig. 4. A cross-section through the fruit-body of *S. rugosum* showing multi-zonate hymenium. (×66.)
Fig. 5. A cross-section through a canker showing an advanced stage of decay; the exposed heartwood is partially decayed showing a narrow decayed zone of advance beyond which the heartwood and the sapwood appear perfectly sound. The callus ridge will be seen to exclude the sapwood near the edge from decay.
Fig. 6. Transverse section through heartwood of oak showing advanced stage of decay. (×66.)
Figs. 7, 8. Parts of tangential longitudinal sections through decayed heartwood of oak showing the presence of hyphae within fibres, wood parenchyma and ray cells. (×66.)

Plate 9

Fig. 1. Culture of *S. rugosum*, 21 days old, on potato-dextrose agar at 23° C. in darkness.
Fig. 2. Culture of *S. rugosum*, 14 days old, on malt agar at 23° C. in darkness.
Fig. 3. Culture of *S. rugosum* on heartwood-blocks of oak for testing decay resistance in the laboratory.
Fig. 4. Culture of *S. rugosum* on sapwood-blocks of oak for testing decay resistance in the laboratory.
Fig. 5. Heartwood blocks of oak showing decay after 4 months' exposure to *S. rugosum*.
Fig. 6. Inoculation on trunk of healthy oak showing experimental infection 4 months after inoculation.
Fig. 7. Experimental infection of oak, 9 months after inoculation with *S. rugosum*.
Fig. 8. Cross-section of oak through the same area of infection, showing the cavity and rot in the sapwood.

PROCEEDINGS, 1955

MEETINGS

8 January 1955. Meeting held at Birkbeck College, London, W.C. 1, at 11.0 a.m. The President, Dr L. E. Hawker, in the Chair.

M. R. Scott. Observations on the biology of *Sclerotium cepivorum*.

A study has been made of the biology of *Sclerotium cepivorum*, the causal organism of Onion White-Rot, in particular of its growth, survival and spread in the soil.

When introduced as mycelium no growth of *S. cepivorum* took place in unsterile soil, except to a limited extent from onion tissue containing actively growing mycelium. The fungus grew in sterile soil, although very slowly and sparsely. Under these conditions growth was improved by the addition of sand and organic supplements such as maize and sucrose. The introduction of soil micro-organisms into sterile soil inhibited the development of *S. cepivorum*. It was concluded that the inability of the fungus to colonize unsterile soil is due to the unsuitability of soil as a growth medium, both nutritionally and physically, and to the antagonism of the soil microflora.

In contrast to the inability of the mycelium to grow and to survive in unsterile soil, sclerotia were highly persistent for periods up to 13 months, except under conditions of high moisture content (100% water-holding capacity), high temperature and organic supplements, when bacterial decay occurred. Sclerotia introduced into soil from cultures were dormant but could be induced to germinate by artificially abrading their surface. Sclerotia removed from soil after a period of 3 months or more germinated when replaced in soil but did not do so for at least a year if left undisturbed. Sclerotium germination was not stimulated by the presence of onion roots.

Spread of White-Rot was retarded by increasing plant to plant spacing. The root system was the part of the plant first infected by the parasite, and spread was eliminated entirely when root contact was prevented by enclosing the root system in a fabric penetrable by the fungus but not by onion roots.

H. Tribe. Studies on the parasitism of *Sclerotinia trifoliorum* Erikss. by *Coniothyrium minitans* Campbell.

Coniothyrium minitans Campbell was isolated from sclerotia of *Sclerotinia trifoliorum* Erikss. from Essex in 1952. It attacked *S. trifoliorum*, *S. sclerotiorum* and *S. minor* in culture, but not *S. gladioli* nor *Botrytis fabae*. It was parasitic on all parts of *S. trifoliorum*; the mycelium invaded the latter with no evidence of antibiotic action. Its distribution on samples of sclerotia obtained from diseased clover fields was studied in 1953 and 1954. In 1953, the samples came from East Anglia, and 30% of these samples yielded some infected sclerotia. In 1954, most of the samples came from the south of England outside East Anglia, and no *Coniothyrium* was found on these. The artificial inoculation of sclerotia buried in unsterile soils was studied in pots and also in boxes set into the field. Using an amendment prepared from cultures of *Coniothyrium* grown in corn-meal sand, mixed thoroughly into soil in 1% concentration, 86–99% of all sclerotia were parasitized within 9–11 weeks in both clay and sandy soils. Where the amendment was applied superficially, there was a lesser degree of control, 8–36% of the sclerotia being parasitized. The possibilities of the use of *Coniothyrium* for biological control of clover rot were discussed.

Miss B. L. Brady. Observations on the life histories of species of *Entyloma*.

The great variety of aerial sporidia described in the literature for *Entyloma* can broadly be classified into three groups on the basis of their shape, consisting of 'needle-shaped',

allantoid, and 'half-moon-shaped' types, the last two being discharged by the drop-excretion mechanism.

The 'half-moon-shaped' sporidium, which is bi-nucleate, and germinates to give a mycelium with clamp-connexions (Stempell, 1935) was collected from leaves infected with *Entyloma* in five out of seven species of *Entyloma* examined, but was also found on pustules of rusts and other smuts, and on healthy leaves of a variety of plants. A comparison of the growth in culture of these sporidia isolated from *E. calendulae* (Oudem.) de Bary on *Calendula officinalis*, and from other sources, with the parasitic mycelium of the *Entyloma* and the mycelium obtained in culture from its germinating chlamydospores, led to the conclusion that this type of sporidium is a ballistospore of an independent fungus closely approximating to Derx's *Intersonilia perplexans* (Derx, 1948), and not connected with the life cycle of the *Entyloma*.

Species of *Tilletiopsis* are almost always collected in ballistospore deposits from diseased and healthy leaves, and ballistospores were collected which agreed fairly closely with Nyland's descriptions of *T. washingtonensis* and *T. minor*. In shape and measurements the ballistospores of *T. washingtonensis* cannot be distinguished from the allantoid sporidia of *E. calendulae*, and it is only in the mycelium formed when the two kinds of spore germinate that they can satisfactorily be separated. It is therefore possible that species of *Tilletiopsis* have occasionally been described in the literature as stages in the life cycle of *Entyloma* species.

The 'needle-shaped' type of sporidium was collected in scrapings of the surfaces of leaves infected by *E. calendulae*, and was found to be bi-nucleate. It is produced when the chlamydospores germinate, after the fusion of the promycelial branches, as illustrated by Kaiser (1936).

J. Webster. Ecology of fungi decomposing cocksfoot stems. *J. Ecol.* (in the Press).

G. J. Cunnell. Two species of *Stagonospora* and their probable perfect stages.

Pycnidia of *Stagonospora typhoidearum* (Desm.) Sacc. and a species of *Leptosphaeria* have been found repeatedly on dead leaf bases of *Typha* spp. at and below water-level. Single spores from both kinds of fruit body gave rise to indistinguishable colonies on 2% malt agar. At the edge of the Petri dishes all these colonies produced a few pycnidia which contained typical spores of *S. typhoidearum*.

S. caricinella Brum. has been found on dead submerged leaves of waterside sedges, especially *Carex riparia* and *C. acutiformis*. On re-infected, sterilized pieces of *C. riparia* leaf pycnidia were produced containing large spores, many of them 5-septate and resembling those of *S. caricis* (Oud.) Sacc. Under the same conditions of culture a perfect stage was formed which was also referable to the genus *Leptosphaeria*. Recently this has been found on a dead leaf of *C. acutiformis* in nature.

Evidence is thus provided for linking the perfect and imperfect stages in these two fungi. The perfect stages are remarkably similar but can be clearly distinguished by their behaviour in culture and by differences in their *Stagonospora* stages.

L. G. Willoughby. Soil Chytrids, with especial reference to *Septosperma rhizophidii* Whiffen and a Chytrid parasite on *Mucor*.

A multi-operculate monocentric Chytrid has been obtained, parasitic on the chlamydospores of a soil mucor from Richmond Park. This mucor is apparently chitinophilic, and only appears when soil is baited with purified shrimp chitin. Previous records of chytrids parasitizing fungi of the Zygomycetes are by Zopf who recorded *Pleotrachelus fulgens* in the mycelium and gemmae of *Pilobolus crystallinus* in 1884, and by Karling who recorded *Rhizophydium mycetophagum*, epibiotic on the conidiophores and hyphae of an unidentified species of *Choanephora* in 1946.

See also these *Transactions*, **39** (1), p. 135, 1956.

19 March 1955. Meeting held at Birkbeck College, London, W.C. 1, at 10.45 a.m. The President, Dr L. E. Hawker, in the Chair.

Sporulation in fungi

C. T. Ingold and Miss V. J. Cox. The relation of light to sporulation in *Daldinia*.

In *Daldinia* spore discharge under natural conditions is periodic, most spores being discharged during the night and few in the daytime. A study has been made of discharge under controlled conditions. In continuous darkness periodic discharge was maintained for 12 days, but then, although spore output continued, it ceased to be periodic. Return to alternating light (12 hr., 100 f.c.) and darkness (12 hr.) at once re-established the periodicity. In continuous light (100 f.c.) periodic discharge ceased after 2–3 days, but was immediately re-established in alternating light (12 hr.) and darkness (12 hr.). When the fungus was placed under conditions of alternating light and darkness each of 6 hr., duration, two peaks of spore-output were soon developed in the 24 hr. period. (See *Ann. Bot., Lond.*, **19**, 201–209, 1955.)

B. E. Plunkett. The aeration complex of factors and fruit body form in Hymenomycetes.

See *Ann. Bot., Lond.* (in the Press).

R. J. W. Byrde. Observations on the sporulation of *Sclerotinia fructigena* on mummified apples and plums in late spring.

Observations were made during April–June, 1951–3, to investigate the influence of climatic factors on outbreaks of sporulation of *Sclerotinia fructigena* Aderh. & Ruhl. on overwintered mummified apples and plums.

The mummified fruits were detached from the trees, and kept for convenience in a single layer on cellulosed wire-netting trays 2 ft. above the open ground. Each morning the production of fresh pustules was assessed on an arbitrary scale ranging from 0 (none) to 3 (heavy). Under favourable conditions, conidial pustules developed overnight: they were at first white, but gradually assumed the characteristic buff colour.

An examination of conventional meteorological records at Long Ashton showed that, on each occasion when fresh sporulation had occurred, the rainfall during the preceding 24 hr. period had exceeded 0·16 in. It is suggested that appreciable rainfall is needed to moisten the normally desiccated mummified fruits, and enable the fungus to resume growth. In addition, rainfall may have a secondary role in increasing atmospheric humidity, thus delaying subsequent drying of the tissues.

Examination of temperature data for all 24 hr. periods when rainfall exceeded 0·16 in. showed that there was a highly significant correlation between minimum overnight temperature and the sporulation index recorded at the end of the period. No sporulation was observed following any night with a minimum temperature of less than 47° F. Maximum day temperatures, and also sunshine data, appeared to bear little relationship to sporulation records. It is suggested that light intensities at this time of year are adequate, even on cloudy days, to initiate sporulation given suitable conditions of rainfall, humidity and temperature.

The weather conditions leading to outbreaks of sporulation were generally associated with either a slow-moving shallow low-pressure system over the British Isles or a moist south-westerly airstream of tropical or subtropical origin.

B. H. Kirsop. Sporulation in yeast.

G. Hadley. The sporulation of *Penicillium notatum* in submerged culture.

A system in which *Penicillium notatum* produces large numbers of phialides and conidia in submerged culture has been selected for the study of the physiology of asexual sporulation.

Standard spore suspensions are inoculated into 25 ml. aliquots of a sucrose mineral salts medium in 100 ml. Erlenmeyer flasks. Such cultures are incubated at 25° C., in a reciprocating shaker (125 cyc./min.) and attain maximum growth in about 72 hr. Sporulation occurs only when calcium ions are added to the medium, the spore number rising to a maximum of about 10 million/mg. dry weight produced as the calcium level is raised to 36 p.p.m. or more. Strontium or barium ions can replace calcium in this system but are less efficient; at equivalent concentrations the order of decreasing activity is calcium, strontium and barium.

Sporulation is not restricted to any limited period but follows mycelial development throughout growth. The time of initial sporulation depends on the inoculum load. With loads of less than $1{\cdot}5 \times 10^5$ spores/ml., the time of sporulation is inversely proportional to the logarithm of the inoculum load, sporulation beginning when the dry weight produced is less than 0·5 mg. With inoculum loads of $1{\cdot}5 \times 10^5$ spores/ml. or more sporulation always begins 17·5 hr. after inoculation, irrespective of the inoculum load, and this time is apparently a genetic minimum under the conditions employed. In cultures where sporulation begins after 17·5 hr. the dry weight at this time depends directly on the inoculum load.

Extracts of mycelium and medium from sporulating cultures have been tested for activity in inducing or hastening sporulation in other *P. notatum* cultures, so far with negative results.

A. G. Morton. Experiments on the production of conidia by *Penicillium griseofulvum.*

The experiments were concerned with the factors which induce vegetative mycelium to form conidia. *P. griseofulvum* was selected as convenient experimental material because the conidia give almost 100% germination in fresh nutrient medium but do not ordinarily germinate in the culture filtrate of a growing culture.

There is a marked difference in behaviour between submerged and surface cultures of the fungus. In submerged culture conidia formation depends very markedly on the composition of the nutrient medium. No sporing takes place in a synthetic nitrate medium when purified glucose is the carbon source unless very high concentrations of glucose are added. With crude glucose, however, sporing takes place abundantly within 24 hr.

The formation of spores in crude glucose has been shown to depend on the presence of some substance which can be removed from crude glucose by appropriate exchange resins.

With low concentrations of glucose (1% and less) no sporulation occurs in submerged culture, either with crude or purified glucose.

In surface culture conidia formation takes place equally well on crude or purified glucose, and at high or low concentrations of carbohydrate. Thus in surface culture some over-riding factor induces sporulation in nutrient conditions which prevent it in submerged mycelium. This factor is possibly connected with the emergence of hyphae from the substrate into the atmosphere.

The effect on conidia formation of continuously raising the nutrient level has been investigated, as well as the effects of the exhaustion of particular nutrients. The possibility that the fungus itself produces metabolites in the culture fluid which induce sporulation has been investigated but seems unlikely.

P. W. Brian. A relation between sporulation and griseofulvin production by some species of *Penicillium.*

See *Trans. Brit. mycol. Soc.* **38**, 305–308, 1955.

THE SPRING FORAY

Pendley Manor, Tring, Herts, 11 to 15 May 1955

By F. B. HORA, *Foray Secretary*

This was the twenty-sixth Spring Foray, and we were very well accommodated at the Manor. Grateful thanks are due to the staff there for the high standard of comfort and good food. About twenty-four members attended, a few spending an odd night or so at nearby hotels. There is no longer a village of Pendley. A former owner of the Big House, wishing to increase his own property could only do so by appropriating the surrounding land of the Pendley villagers. This was done and the village obliterated. We have progressed since those days, and to-day the Manor is a flourishing adult education centre.

Members arrived on the Wednesday with a goodly sprinkling of cars, so that subsequent transport presented no problems. The Ashridge area of Berkhamsted Common, Aldbury Common and Sallow Copse were visited on Thursday, and Wippendell Wood (near Watford) on Friday. On Saturday, King's Wood and Stockgrove Wood near Heath and Reach (in Bedfordshire) were searched and, finally, on Sunday we visited the gravel pits at Bourne End. Collecting conditions were, in general, good, there being little inconvenience from rain, and the Foray as a whole was most rewarding, particularly to searchers of the Ascomycetes. Good material of *Actidium hysterioides* was found. Dr Webster reports that this appears to have been last collected in 1861 by Currey. Mr Colin Booth has examined Currey's specimen and says it is rather immature. Ainsworth and Bisby, in their Dictionary, query whether *Actidium* is an Ascomycete, whilst Bisby and Hughes do not describe it in their Summary of the British Hysteriales (these *Transactions*, **35**, 308 (1952)). The present gathering has well-developed asci. Mr Graddon did particularly well with Discomycetes. He notes that *Sclerotinia hirtella* was known previously only from single isolated specimens, and he was very pleased to confirm its status by finding some dozens of specimens at one place. He believes the Foray yielded *Ciborinia foliicola* as the first British record. A 'particularly memorable' moment for him was the finding together in the same heap of pine needles, *Desmazierella acicola* and *Hyalotricha trichoidea*. *Stictis stellata* was another good find. Amongst the Agarics, two new records were made: *Pluteus satur*, closely related (perhaps too closely) to *P. phleborphorus* and *Omphalia cylindrico-campanulatus*. This was first described from Java and is very close to *O. picta* Fr. The cap and gill shape are most unusual, and an account is being prepared for publication.

No one should leave Pendley Manor without seeing the Pendley Pottery which is made entirely on the premises. We were very privileged to be shown a demonstration of the art from the mixing of the clay to the final firing. Many members purchased examples.

For help with the preparation of this report, it is a pleasure to thank Dr Agnes Brown and Miss Grace Waterhouse, Messrs Colin Booth, W. D. Graddon and Derek Reid, Drs Parker-Rhodes and Webster. I am particularly grateful to Mr Derek Reid for acting as local Secretary. The accompanying lists follow conventional lines. For nomenclature, see these *Transactions*, **38**, 185 (1955).

List of species

A. = Ashridge Park Woods, including Sallow Copse; *Ald.* = Aldbury Common (in Ashridge area); *B.* = Bourne End gravel pits; *H.* & *R.* = Kings Wood or Stockgrove Wood without specifying which; *K.* = Kings Wood, near Heath and Reach; *P.* = woods and grounds of Pendley Manor; *R.* = Ringshall (in Ashridge area); *S.* = Stockgrove Wood, near Heath and Reach; *T.* = Tring Station and surroundings; *W.* = Wippendell Wood, near Watford. Voucher material: [1] = in herb. Kew; [2] = in herb. University of Sheffield. † = new British record.

MYXOMYCETES

Arcyria ferruginea, *S.*
Ceratiomyxa fruticulosa, *B.*
Reticularia lycoperdon, *Ald.*

PHYCOMYCETES

Perenospora alsinearum Casp., on *Cerastium vulgatum*, *B.*, *K.*; on *Stellaria media*, *K.*; aparines (de Bary) Gäum. (*P. calotheca f. aparines* de Bary), *B.*, on *Galium aparine*, *K.*; ficariae Tul., on *Ranunculus acris*, *P.*, on *R. repens*, *S.*; parasitica (Fr.) Tul. (*P. dentariae* Rabenh.), on *Cardamine pratensis*, *A.*; ranunculi Gäum., *B.*, *S.*; trivialis Gäum., *B.*, *S.*; trifoliorum de Bary, *B.*; verna Gäum. (*P. grisea* Ung.), on *Veronica serpyllifolia*, *S.*; viciae (Berk.) de Bary, on *Vicia hirsuta*, *B.*
Synchytrium mercurialis (Lib.) Fuckel, on *Mercurialis perennis*, *K.*

EU-ASCOMYCETES

Pyrenomycetes

[2]Actidium hysterioides, on *Pinus* wood, *K.*
Anthostoma turgidum, on *Fagus*, *P.*
[2]Anthostomella tomicum, on *Calamagrostis epigeios*, *S.*
Calyculosphaeria tristis, on *Diatripe stigma* on *Ulmus*, *P.*
Chaetomium elatum, on unidentified herbaceous stem, *R.*
[2]Chaetosphaeria innumera, on *Crataegus monogyna*, *A.* (conidial), on rotten wood of *Acer*, *A.*, on *Quercus*, *S.*
Cryptodiaporthe salicella, on *Salix*, *B.*
Cryptosphaeria eunomia, on *Fraxinus*, *S.*
Cryptospora betulae, on *Betula*, *K.*
Diaporthe leiphaemia, on *Quercus*, *S.*
[2]Diaporthopsis angelicae, on *Heracleum sphondylium*, *B.*
Diatrypella favacea, *A.*
Hypomyces rosellus (conidial), on conifer bark, *S.*, on *Pinus*, *W.*
Hypocrea pulvinata, on *Polyporus betulinus*, *S.*
Hypoxylon fragiforme (Pers. ex Fr.) Kickx (H. coccineum Bull.), on *Crataegus* and *Fagus*, *A.*; rubiginosum (conidial) on ?conifer, *S.*
Lasiosphaeria ovina, on dead wood, *W.*; spermoides, on rhizomorphs of *Armillarea mellea* on rotten wood, *P.*
[2]Leptosphaeria graminis, on *Phragmites communis*, *S.*; microscopica, on *Glyceria maxima*, *B.*, nigricans (Rob. in Desm.) Ces. & de Not., on barley stubble, *T.*, on *Dactylis glomerata* and *Deschampsia caespitosa*, *K.*; [2]typharum, on *Typha latifolium*, *B.*
Lophiotrema semiliberum, on *Agropyron repens*, *T.*
Lophodermium arundinaceum, on *Agropyron repens*, *A.*
Melanomma fuscidulum, on *Sambucus*, *B.*; pulvis-pyrius, *B.*; subdispersum (conidial), on *Betula* bark, *K.*, *S.*

Microthyrium culmigenum Sydow, on *Holcus mollis*, *K.*
[2]Nectria inventa (conidial), on grass, *T.*
[2]Ophiobolus herpotrichus, on *Agropyron repens*, *B.*, *T.*, *W.*; rubellus, on unidentified herb, *T.*
Ophionectria cerea (Berk. & Curt.) Ellis & Everh. (conidial), on *Fagus*, Ashurst.
Phyllachorea graminis, on *Zerna ramosa*, *T.*
Pleomassaria siparia, on *Betula*, *K.*
[2]Pleospora trichostoma (Fr.) Fuckel, on barley stubble, *T.*
Pseudovalsa lanciformis, on *Betula*, *K.*
Rhopographus pteridis, on *Pteridium aquilinum*, *A.*, *K.*
[2]Trichosphaeria myriocarpa, on *Crataegus*, Ivinghoe.
[2]Tubeufia helicomyces von Höhnel (conidial), on *Deschampsia caespitosa*, *K.*

DISCOMYCETES

Acetabula leucomelas, *H.* & *R.*
Aleuria repanda, *H.* & *R.*; sepiatra, *B.*
Allophylaria chrysostigma (Fr.) Nannf., *W.*
Apostemidium guernisaci, *B.*; fiscellum Karst., *B.*
Belonopsis pilosa (Crossl.) Rehm, *H.* & *R.*
Botryotinia fuckeliana (de Bary) Whetzel, *H.* & *R.*
†Ciborinia foliicola (Cash & Davidson) Whetzel, on *Carex*, *B.*
Ciliaria scutellata, *B.*
Dasyscypha acutipila, *B.*; albotestacea (Desm.) Massee, *B.*; carneola, *B.*; clandestina, *A.*; diminuta, on *Juncus*, *B.*, *H.* & *R.*; grevillei, *A.*, *B.*; inquilina (Karst.) Winter, *B.*; leucophaea (Pers.) Massee, *B.*; nidulus (Schmidt & Kuntze) Massee, *B.*; nivea, *H.* & *R.*; pudicella, on *Agropyron repens*, *B.*; virginea, *Ald.*
Desmazierella acicola, *H.* & *R.*
Helotium conigenum sensu Karsten, *H.* & *R.*; cyathoideum (Bull.) Karst., *Ald.*; repandum, *B.*
Hyaloscypha dematiicola (Berk. & Broom) Nannf. (conidial), on rotten wood, *A.*, *S.*, on *Acer*, *A.*; hyalina, *W.*; leuconica (Cooke) Nannf., *H.* & *R.*; stevensoni (B. & Br.) Nannf., *H.* & *R.*
Hyalotricha trichoidea (Phill. & Plowr.) Dennis, H. & *R.*
Lophodermium arundinaceum (Schrad.) Chev., *B.*; pinastri (Schrad.) Chev., *H.* & *R.*
Mollisia cinerea, *H.* & *R.*; dilutella Fr., *H.* & *R.*; minutella Rehm, *H.* & *R.*
Ombrophila clavus *var.* grandis Boud., *H.* & *R.*
Polydesmia pruinosa, *Ald.*
Rhytisma acerinum, on *Acer*, *A.* (good development of asci).
Sclerotinia curreyana, *B.*; hirtella, *Ald.*
Stictis stellata, *B.*
?Tapesia callunae Vel., *Ald.*; lividofusca (Fr.) Rehm, *Ald.*
Unguicularia incarnatina (Quél.) Nannf., *B.*; scrupulosa (Karst.) von Höhnel, *Ald.*

HETERO-BASIDIOMYCETES

Tremellales

Exidia nucleata, *Ald.*; spiculosa (Gray) Sommerf., on *Fagus*, *S.*

Calocerales

Dacrymyces stillatus, on *Sambucus*, *W.*

Uredinales

Cumminsiella mirabilissima, on *Mahonia aquifolium*, *P.*
Phragmidium sanguisorbae, on *Poterium sanguisorbae*, *B.*
Puccinia adoxae, on *Adoxa moschatellina*, *K.*; buxi, on *Buxus sempervirens*, *P.*; caricina, O, I, on *Urtica dioica*, II, III, on *Carex* (dead), *B.*; obtegens, on *Cirsium arvense*, *B.*, *K.*, *P.*; violae, on *Viola* sp., *W.*
Trachyspora intrusa, on *Alchemilla vulgaris*, *W.*

Tranzschelia anemones, on *Anemone nemorosa*, *K.*
Uromyces dactylidis, O, I, on *Ranunculus repens*, II, III, on *Dactylis glomerata*, *B.*, on *R. ficaria*, *K.*; ervi, I, III, on *Vicia hirsuta*, *B.*; ficariae, on *R. ficaria*, *B.*

USTILAGINALES

Urocystis anemones (with *Tranzschelia anemones* on same leaf), *K.*
Ustilago tragopogon-pratensis, *T.*

HOMO-BASIDIOMYCETES—HYMENOMYCETES

APHYLLOPHORALES

(1) *Porohydnineae*

Corticium centrifugum (Lév.) Bres., type and forms on lichenous twigs, *W.*; confine, on *Abies*, *S.*; illaqueatum Bourd. & Galz., on twigs, *R.*; lacteum Fr. (non Bourd. & Galz.), on leaves of *Juncus*, *S.*; laeve, on *Pinus*, *S.*; sphaerosporum R. Maire, on *Pteridium*, *Br.*, *K.*, *W.*
Cyphella capula, *S.*; *var.* flavescens, on herbaceous stems, *B.*; sulphurea Fr., *S.*
Daedalea confragosa, *Ald.*, *R.*, *S.*; quercina, *K.*
Fomes annosus, *Ald.*
Ganoderma applanatum, on stump of ?*Quercus*, *R.*
Gloeocystidium contiguum (Karst.) Bourd. & Galz., on *Salix*, *B.*; lactescens (Berk.) v. H. & L., on coniferous stick, *S.*; porosum (Berk. & Curt.) Wakf., *A.*, *W.*; tenue (Pat.) v. H. & L., *S.*
Grandinia helvetica, on *Typha*, *B.*
Odontia bicolor, *W.*; arguta, *B.*
Pellicularia bispora (Bourd. & Galz.) Rog., on *Epilobium*, *B.*; botryosum (Bres.) Rog., on *Pinus*, *S.*; subcoronata (v. H. & L.) Rog., *W.*; vaga (Fr.) Rog., on dead wood, *R.*
Peniophora byssoidea, *S.*; cinerea, on *Prunus*, *B.*; gigantea, *K.*; hydnoides *S.*; incarnata, *R.*; leprosa, *A.*, *Ald.*, *R.*; longispora, on *Betula*, *A.*; mollis (Bres.) Bourd. & Galz., on *Betula*, *K.*; nuda, *B.*; pallidula, on coniferous twigs, *R.*, *S.*, *W.*; pubera, *A.*, *W.*
Polyporus adustus, on *Fagus*, *A.*, *R.*, on *Betula* and *Quercus*, *K.*; betulinus, on *Betula*, *S.*; brumalis, *A.*, *Ald.*; fumosus, on *Fagus*, *R.*; lacteus, on *Pinus*, *W.*
Polystictus abietinus, on *Pinus*, *K.*, *S.*; versicolor, *A.*, *R.*
Poria calcea (Fr.) Bres., on *Larix*, *W.*; mucida (forms), *R.*, *K.*, *W.*, on old stump, *A.*; xantha Fr., on *Pinus*, *W.*
Radulum orbiculare, *S.*
Solenia anomala, *S.*
Stereum hirsutum, *A.*, *K.*; rugosum, on sticks, *R.*; spadiceum, on bark of *Fagus*, *W.*
Trametes gibbosa, on *Betula*, *K.*; subsinuosum Bres., on *Abies*, *S.*

(2) *Clavariineae*

Pistillaria culmigena, *B.*, micans, *B.*; setipes Grev., on dead grass, *K.*

AGARICALES

Armillaria mellea (rhizomorphs), *W.*
Bolbitius vitellinus, *K.*
Collybia fusipes, on foot of old *Fagus* stump, *R.*
Coprinus micaceus, on *Fagus*, *A.*; radians, on *Fagus*, *A.*
Entoloma clypeatum, on grassy paths, *K.*; sericeum, in grassy places, *A.*
Galera hypnorum, among mosses, *K.*, *S.*; mycenopsis, on mossy bank, *B.*; tenera, on grassy path, *R.*
Hypholoma fasciculare, *Ald.*, *K.*, *P.*
Marasmius esculentus *sub.sp.* pini Singer, on buried cones of *Pinus*, *K.*, *S.*
Mycena acicula, *B.*; haematopus, on *Castaneus*, *Ald.*; olida, *R.*; pseudo-crispula Kühner, on *Juncus*, *K.*; quisquiliaris, *B.*; speirea, on twig of *Quercus*, *R.*
†Omphalia cylindrico-campanulatus (P. Henn.) v. Höhnel, on *Fagus*, *W.*
Panaeolus ater Kühner & Romagn., in grassland, *S.*

Panus stipticus, *K.*
Pholiota sphaleromorpha, on grassy path, *S.*; togularis sensu Lange, *S.*
Pluteus cervinus, *P.*, *W.*; [1]†satur Kühner & Romagnesi, *B.*
Tricholoma carneum, *B.*; gambosum, *W.*

GASTEROMYCETES

Lycoperdon pyriforme, on dead standing tree, *W.*
Phallus impudicus (rhizomorphs), *A.*
Sphaerobolus stellatus, on herbaceous remains, *B.*

FUNGI IMPERFECTI

COELOMYCETES

Cryptomela typhae, *B.*
Discella carbonacea, *B.*
Wojnowicia graminis, on barley stubble, *T.*

HYPHOMYCETES

Acrothecium simplex, *S.*
Aegerita candida, *S.*
Arthrinium curvatum, Kunze ex Fr., on *Carex* sp., *K.*; puccinioides (DC.) Kunze ex Fr., on *Deschampsia caespitosa*, *K.*
Coniothecium amentacearum, *B.*
Oidium aureum Link, *W.*; conspersum (Link) Linder, *Ald.*
Periconia hispidula (Pers. ex Fr.) Mason & Ellis, on *Carex* Sp., *S.*
Tetracladium marchalianum, *P.*, *S.*
Torula herbarum, *B.*
Triposporium elegans, *Ald.*

THE TWENTY-NINTH ANNUAL PLANT PATHOLOGY FIELD DAY

24 June 1955

The Director, Dr F. R. Tubbs, welcomed more than 70 members and guests at East Malling Research Station, Kent, on 24 June 1955. Dr R. V. Harris then described the aims of the Plant Pathology Section.

Before lunch members were shown work on fungicides and virus diseases which included methods used to inoculate apple rootstocks uniformly with powdery mildew and to test fungicides for its control; experiments on the chemotherapy of silver leaf disease; exhibits of virus diseases of strawberries, fruit trees and hops, and examples of the methods used to produce virus-free plants. In the afternoon parties visited the laboratories and glasshouses and were shown work on the biochemical factors influencing the susceptibility of apple and pear to *Venturia inaequalis* and *V. pirina*: the mechanism of resistance to Verticillium wilt in hops; the morphology of an *Endogone* sp. associated with the roots of strawberry and other plants; the etiology of cauliflower disease of strawberry and the methods in use for measuring and reducing the leaf inoculum responsible for autumn infections of the bacterial canker disease of cherry.

After tea the President expressed the thanks of the visitors to the Director and Dr Harris for the hospitality shown to the Society; to Dr Crosse for the excellent organization, and to all who had taken such trouble to provide a most instructive and enjoyable meeting.

J. M. HIRST
Secretary, Plant Pathology Committee

ANNUAL GENERAL MEETING

Saturday, 10 December 1955. The fifty-ninth Annual General Meeting was held in the rooms of the Linnean Society of London at 12 noon, with the President, Dr L. E. Hawker, in the Chair.

After the minutes of the previous Annual General Meeting had been read and signed, the President recorded with regret the deaths during the year of Miss D. M. Cayley, Dr E. J. Gilbert, Mr J. Rees and Mr D. W. Davies. She then reported briefly on the year's activities.

The Treasurer presented his Annual Statement which was accepted *nem. con.*

The following Officers, Council and Committee members were then elected for 1956:
President: W. D. Graddon.
Vice-Presidents: F. B. Hora in addition to past Presidents, L. E. Hawker and S. D. Garrett.
Secretary: J. Webster.
Foray Secretary: F. B. Hora.
Plant Pathology Committee Secretary: J. M. Hirst,
Treasurer: W. Buddin.
Editors: G. C. Ainsworth, S. D. Garrett.
New Members of Council: Miss J. Fraymouth, P. H. Gregory, T. J. Wallace (to replace P. W. Brian, C. L. Duddington, J. T. Palmer).
New Members of Plant Pathology Committee: R. V. Harris, H. Owen, D. C. Gwynne.
New member of Foray Committee: Mrs S. M. Francis.

Five new members and one Associate were then elected, making a total of thirty-nine new members and three Associates for the year. A brief discussion of the programme for 1956 followed.

The Annual General Meeting agreed to join in a protest to the Postmaster-General concerning his decision to increase postal charges on books and periodicals.

A telegram of congratulations from the meeting was sent to Mr H. M. Ridley on the occasion of his hundredth birthday.

At 2·30 p.m. the President gave her address on 'The experimental control of form and phase in fungi'. The meeting concluded with a vote of thanks to the President, proposed by Dr B. E. Plunkett.

RECEIPTS AND PAYMENTS for the year ended 30 June 1955

RECEIPTS

	£ s. d.	£ s. d.
1st July 1954, Balance brought forward ...		2392 7 4
Cambridge University Press sales:		
Transactions, Vol. 37	909 5 6	
Reprints	203 10 10	
Back Volumes	144 15 2	
50-year *Index* and *Lichen Catalogue*	39 8 3	
Miscellaneous	1 10 8	
List of Common Brit. Pl. Diseases	2 18 6	
		1301 8 11
Sales:		
Diseases of Brit. Grasses, etc		78 3 4
Sundry sales at Meetings, etc.		15 2 3
Subscriptions:		
Arrears	5 0 0	
Current	840 2 11	
In advance	17 0 6	
Associates	13 10 0	
		875 13 5
Donations:		
Cheesman and Pethybridge Funds	3 10 0	
Plates and Printing Fund	16 15 0	
Hospitality Fund	4 1 9	
		24 6 9
Grants, etc :		
Through Royal Society (1954)	300 0 0	
Imp. Chem. Ind. Ltd. (3rd and final) ...	200 0 0	
A. A. Pearson Bequest (1st moiety) ...	100 0 0	
		600 0 0
Interest:		
Capital Reserve Fund	28 17 6	
Post Office Savings Bank	37 12 8	
		66 10 2
		£5353 12 2

PAYMENTS

	£ s. d.	£ s. d.
Addresses for Jubilee of Ass. of Appl. Biol. and Roy. Hort. Soc.		5 9 3
Cambridge University Press:		
Production, *Transactions*, Vol. 37 (1150 copies)	1357 10 4	
Reprints	206 10 3	
Distribution of Member's copies, etc. ...	47 10 10	
Commissions on:		
Production Vol. 37 and Reprints ...	201 8 11	
Members' copies (2 years)	114 4 0	
Sales of Vols. 1–37 and Misc.	126 6 10	
Sales of *Index* and *Lichen Catalogue* ...	9 17 1	
		2063 8 3
Purchase of Savings Certificates		225 0 0
Sundry Printing		56 1 2
Postages, Stationery, etc.		58 5 9
Fees for Meetings		5 0 0
Subscriptions:		
Woolhope Club	1 0 0	
Biological Council	1 10 0	
		2 10 0
Grants on Cheesman and Pethybridge Funds		11 12 0
Library Purchases, Binding, etc.		41 12 1
Balance:		
At Midland Bank	899 6 0	
In Post Office Savings Bank	1985 7 8	
		2884 13 8
		£5353 12 2

CAPITAL RESERVE FUND (Nominal Values of Stock)

Cheesman & Pethybridge Funds ...	£260 of 3½% War Stock	General, Hospitality, Library and Printing Funds	£365 of 3½% War Stock £550 of Savings Certificates
Lister Fund & Pearson Bequest ...	£500 Saving Certificates		£200 of 3½% Defence Bonds
		GRAND TOTAL ... £1875	

Examined and found correct (*Signed*) W. C. MOORE; (*Signed*) WALTER BUDDIN, *Hon. Treasurer.*

Donations and Grants to the several Funds of the Society are gratefully acknowledged.